UNIVERSITY OF EDINBURGH

The Biology of Megastigmus spp. Dalman (Hymenoptera; Chalcidoidea; Torymidae) with special reference to Distribution & Biological Control.

by

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1952

Thesis submitted for the degree of Ph.D.

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INTRODUCTION

In March 1950 the Head of the Forestry Commission Research Station at Alice Holt Lodge, Surrey, requested that research should be commenced on the distribution in Great Britain of those species of Megastigmus which infect the seed of coniferous trees. This distribution investigation continued under the direction of the entomologist to the Forestry Commission until January, 1952 from which date the whole project was directed by the writer at Edinburgh. In October 1950 the writer commenced studies on the external anatomy of the genus, together with detailed studies on the field bionomics of Megastigmus spermotrophus. Wachtl. at several stations including the Bedgebury National Pinetum, Kent; Rosehaugh Estate, Avoch, Ross; and Novar Estates, Evanton, Ross-shire.

The ensuing account is divided into two parts. Part I comprises a study of the external anatomy of the genus based on M. spermotrophus; M. pinus; and M. dorsalis together with an account of the reproductive organs. Descriptions of the immature stages of Megastigmus and its parasite complex are also included. Part II deals with biological experiments and observations on field bionomics. Special mention is made of those factors, physical and biological, which exert a controlling influence upon the numbers of M. spermotrophus.

Historical Review

Megastigmus, a member of the sub-family Megastigminae of the family Callimomidae of the Chalcidoidea, was first elevated/

elevated to generic rank by Walker in 1833. However Swederus (1795) was the first to describe species of the genus but he placed them in Pteromalus. Then followed a long period of taxonomic confusion much of which persisted until the present day but especially useful papers on the conifer infesting species were published by Crosby (1913), Seitner (1916), Hoffmeyer (1929 et seq.) and Escherich (1938). However, Milliron (1949) succeeded in producing order out of chaos in his paper on the Nearctic species in which he described, on a common system, all the previously known forms of that region. This work has proved invaluable for the identification of those species associated with conifers indigenous to the New World and now introduced here. But for Megastigmus species attacking European trees Hoffmeyer remains the latest authority.

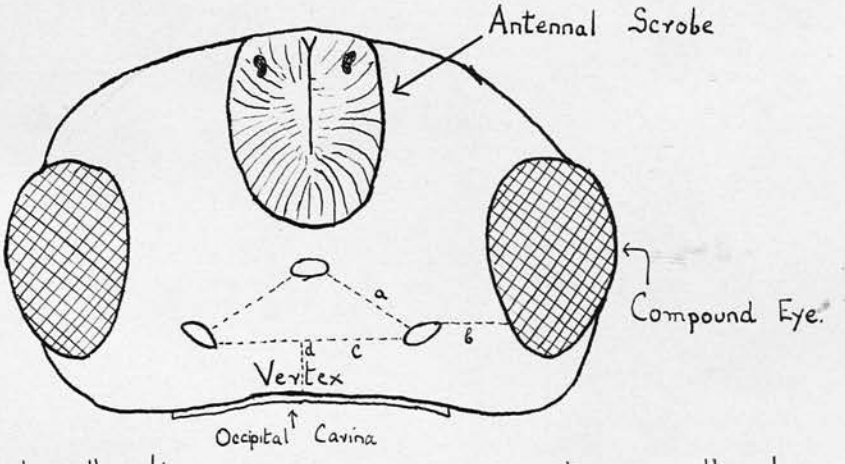
The first biological paper on the genus was by Walker (1845) in which he claimed that M. dorsalis Fabr. was parasitic on a gall-forming Cynipid. From then until the turn of the century a number of other species including M. stigmatizans Fab. were also proved entomophagous and several others erroneously assumed to be so. However the publication by Wachtl (1884 & 1893) of papers in which he claimed that M. spermotrophus & M. pictus. Forst were phytophagous started a long controversy in which Howard (1892) and Riley (1893) participated. However when MacDougall (1906) upheld Wachtl's claim it was generally recognized that some species were in fact truly phytophagous. It is interesting to observe that in 1895 Borries postulated that/

that some species might supplement their animal food by plant material, a situation later found to exist in an Australian form by Noble (1940).

The only available biological accounts of conifer infesting species are by Laidlaw (1931) on M. pinus. Parfitt, Seitner (1916) on M. strobilobius Ratz, Seitner (1916) on M. suspectus. Borries and Miller (1916) & MacDougall (1906) on M. spermotrophus. The most complete biological data on any Megastigmine species is that by Milliron (1949) who studied M. nigrovariegatus. Ashmead a phytophagous species completing its life-cycle in rose-hips.

0·3 m.m.

Fig: 1



a. Lateral ocellar line.

b. Ocellocular line.

c. posterior ocellar line.

d. Ocelloccipital line.

DORSAL ASPECT OF HEAD OF MEGASTIGMUS

PART I.

Chapter I.

The external anatomy of the genus Megastigmus. Dalm.

Apart from an account in Polish on Megastigmus kuntzei (z. Jalowcowy 1946) no work has been conducted on the morphology of a member of this genus. James (1926) however published a comprehensive description of the anatomy of Harmolita, a phytophagous Chalcid which has been used as a background to the present study, which is based upon an examination of three species Megastigmus spermotrophus. Wachtl. M. pinus. Parfitt and M. dorsalis. Fabr. The object of this work was to examine carefully for possible differences in external anatomy between the phytophagous species M. spermotrophus and M. pinus and a parasite form M. dorsalis. James has commented (1926) for instance that "the labium in phytophagous forms compared with the same structure in certain parasitic Chalcidoids which have been described, is more generalized, the paraglossae being represented by a pair of distinct lobes on either side of the ligula, whilst even the latter shows traces of a paired organ".

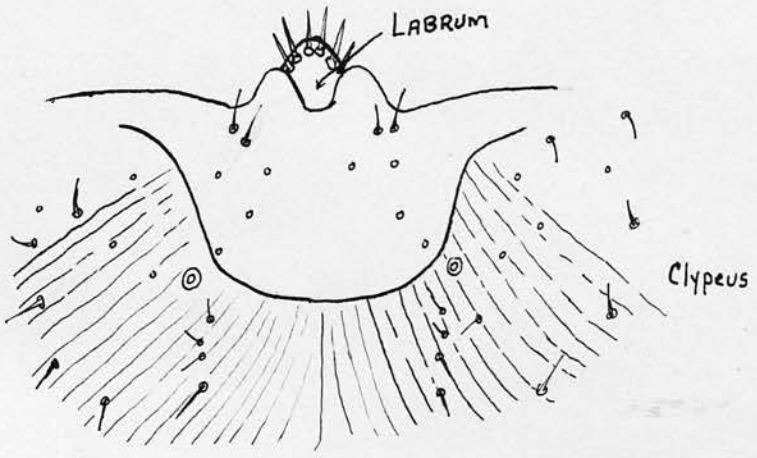
The dissecting medium employed was 10% glycerine and permanent mounts were stained where necessary with Delafield's haemotoxylin. In mounts of chitinized parts the soft material was removed by boiling in 10% KOH for ten minutes and then staining the preparations with 1% acid fuchsin.

The Head

The head is a rounded sub-globose structure, protuberant in front with two deep antennal scrobes (Fig. 1) whilst the posterior surface/

0·1mm

Fig. 2.



DORSAL VIEW OF CLYPEUS OF M. spermotrophus.

surface of the capsule is concave. The whole exterior surface of the capsule is covered with a delicate system of rugulae which tends to run dorso-ventrally except in the region of the vertex where the "stripes" run transversely. Three Ocelli, .08 mm. in diameter, are arranged in an isosoceles triangle on the vertex. The large red compound eyes occupying the lateral margins of the rounded anterior portion of the capsule are prominantly domed.

Sutures between the head sclerites, commonly recognized in more generalized insects, have largely disappeared but it is possible to define the areas of the sclerites by considering their position relative to the fixed structures of the head region. Hence a labrum, clypeus and frons are distinguishable anteriorly; a vertex dorsally; posteriorly the occiput and gular regions; and laterally the compound eyes and genae.

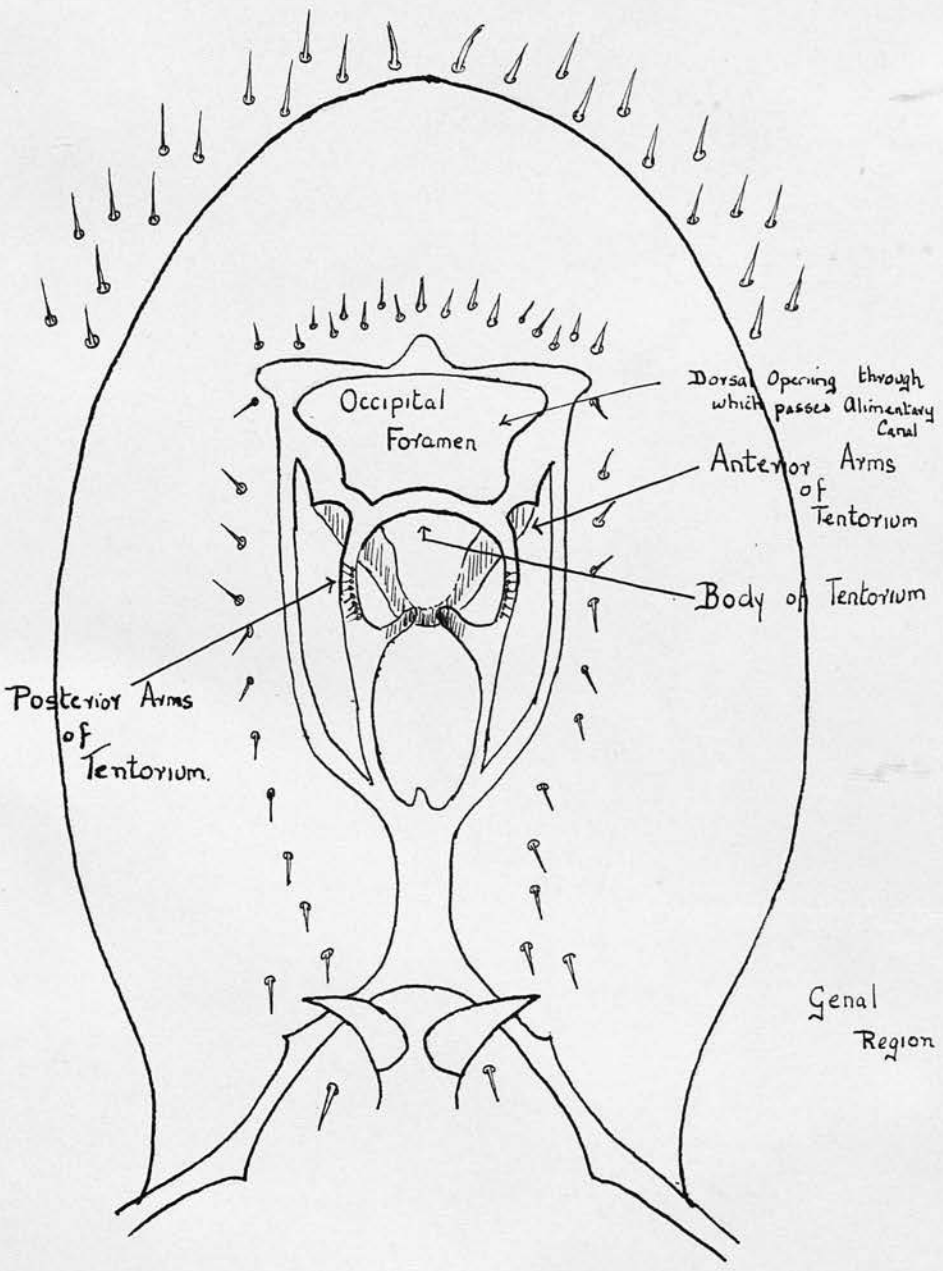
(1) The Labrum

The labrum is an elongate but rounded moveable plate attached to the anterior edge of the clypeus above the mandibles. James (1926) has suggested that in Chalcids it characteristically bears 6 or 7 long stout spines and the structure certainly carries 6 spines in all species of Megastigmus examined.

(2) The Clypeus

The clypeus is a smooth, strongly chitinized band extending along the anterior border of the head capsule. In its central region it is cut out into 2 large, rounded, triangular teeth (Fig. 2) above and lateral to which are a pair of stout bristles.

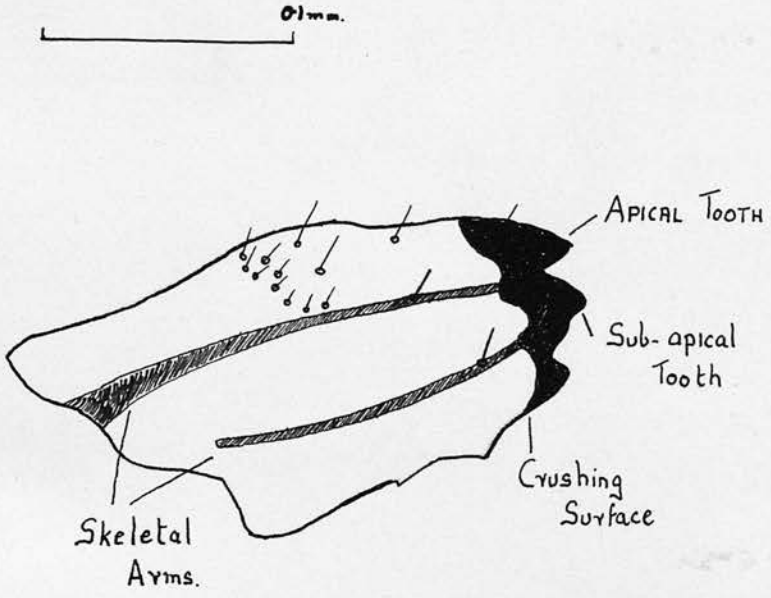
(3)/



POSTERIOR ASPECT OF CERVICAL REGION.
OF M. spermotrophus

Fig: 3

Fig: 4



Mandible of M. spermotrophus

(3) The Frons

In more generalized insects the frons is defined as that region of the head capsule enclosed by the arms of the epicranial suture and by the clypeus. In Chalcids however the suture has disappeared and the frontal sclerite can be defined by diverging lines drawn from the median ocellus to the clypeus but passing only just outside the antennal fossae.

The Endoskeleton of the Head

The tentorium is formed by three pairs of invaginations which are known as the anterior, posterior and dorsal arms of the tentorium respectively. The body of the tentorium is formed by the union of these invaginations and appears as a thick chitinous bar lying across the occipital foramen so as to divide it into two openings. The alimentary canal passes into the head via the dorsal opening whilst the lower admits the nervous system (Fig. 3).

The Mouth-Parts.

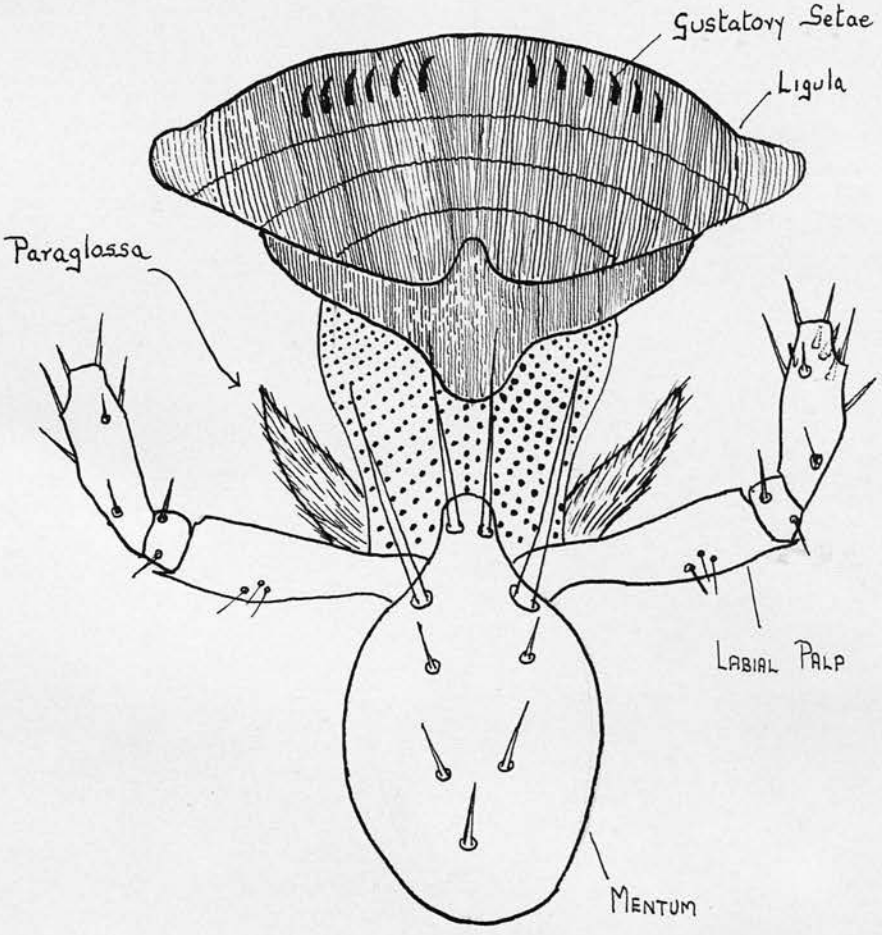
The mouth parts comprise the typical organs of a mandibulate insect although the palpifer segment of each maxillary appendage is united to the stipes without trace of a suture.

(1) The mandibles

The pair of mandibles are very well developed, rather widely wedge-shaped measuring .27 mm. in length x .18 mm. in width. The outer, anterior, convex surface bears a number of setae (Fig. 4) but these are certainly not as long as Jalowcowy reports in the case of M. kuntzei. He depicts two of these setae almost half as long as the entire mandible. On the concave/

0·1mm

Fig: 5



LABIUM OF M. speymotrophus

concave posterior aspect are two conspicuous skeletal rods which arise near the apex of a mandibular tooth and terminate free in the club-like apex. The inner edge of each mandible possesses three marked teeth (the basal the smallest). The insect has not been observed to partake of solid food but they are obviously used to make the neatly rounded hole by which the adult escapes from the seed.

(2) The Labium (Fig. 5).

The labium is connected to the maxillae, between which it lies, by a thin chitinous membrane. It consists of a rather elongate oval plate bearing, distally, the expanded ligula and laterally a pair of delicate lobes - apparently overlooked by Jalowcowy.

A careful examination of the ligula reveals that it is traversed longitudinally by a series of channels which clearly show evidence of its having developed from a paired structure as was observed by James in Harmolita. The distal margin of the ligula is serrated and provided with a mass of very fine hairs. In addition, five or six thick setae arise (on minute protuberances) on each lobe of the ligula and are probably secretory in nature analagous to the basiconic sensillae of Berlese (1909).

The two lateral lobes or paraglossae are densely covered with fine hairs. These structures are extremely delicate and often adopt a position in microscope preparations which renders them almost invisible unless the hairs are detected by careful focussing/

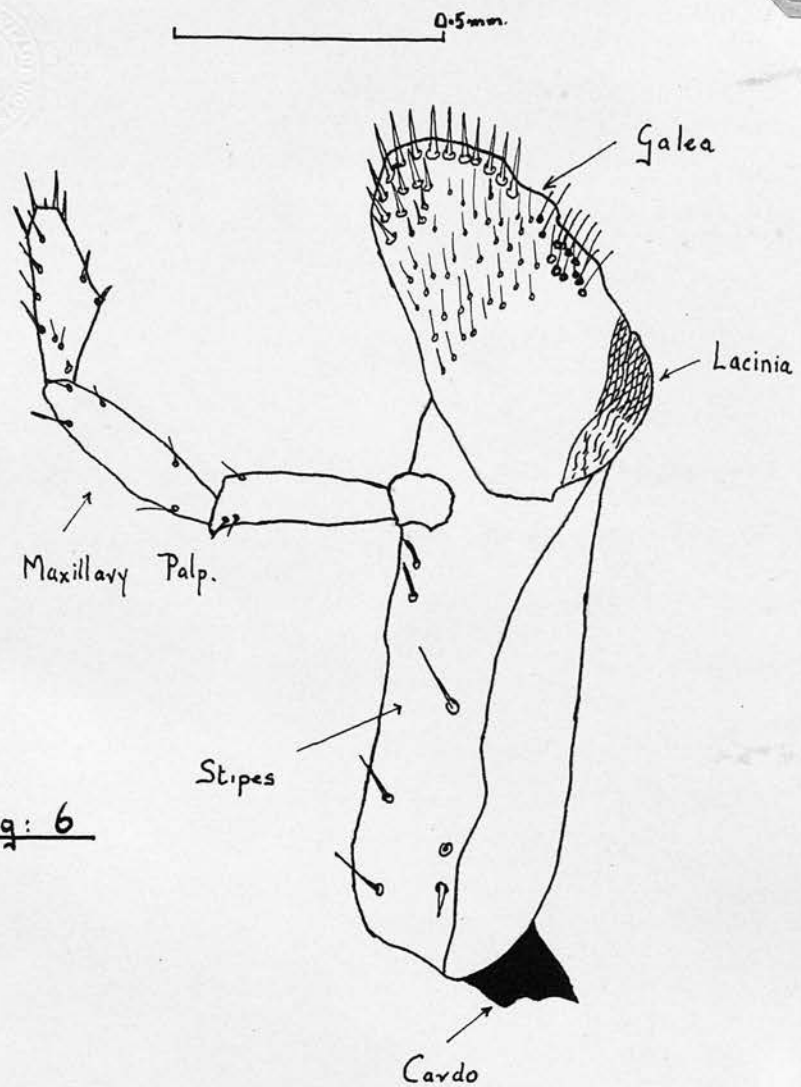


Fig: 6

MAXILLA OF M. spermotrophus.

focussing. The difference between the phytophagous and parasitic forms of Chalcids suggested by James in the organ are not apparent in Megastigmus although the fine hairs covering it in M. pinus and M. spermotrophus are noticeably shorter than in the parasitic species M. dorsalis. The labial palps are given off from the ventral surface of the labial plate. They consist of three segments - the terminal one bearing ten setae towards its apex.

The mentum is elongate distally and bears four stout bristles anteriorly - whilst the membraneous submentum is devoid of setae and articulates with the gular region of the head capsule.

(3) The Maxillae (Fig. 6)

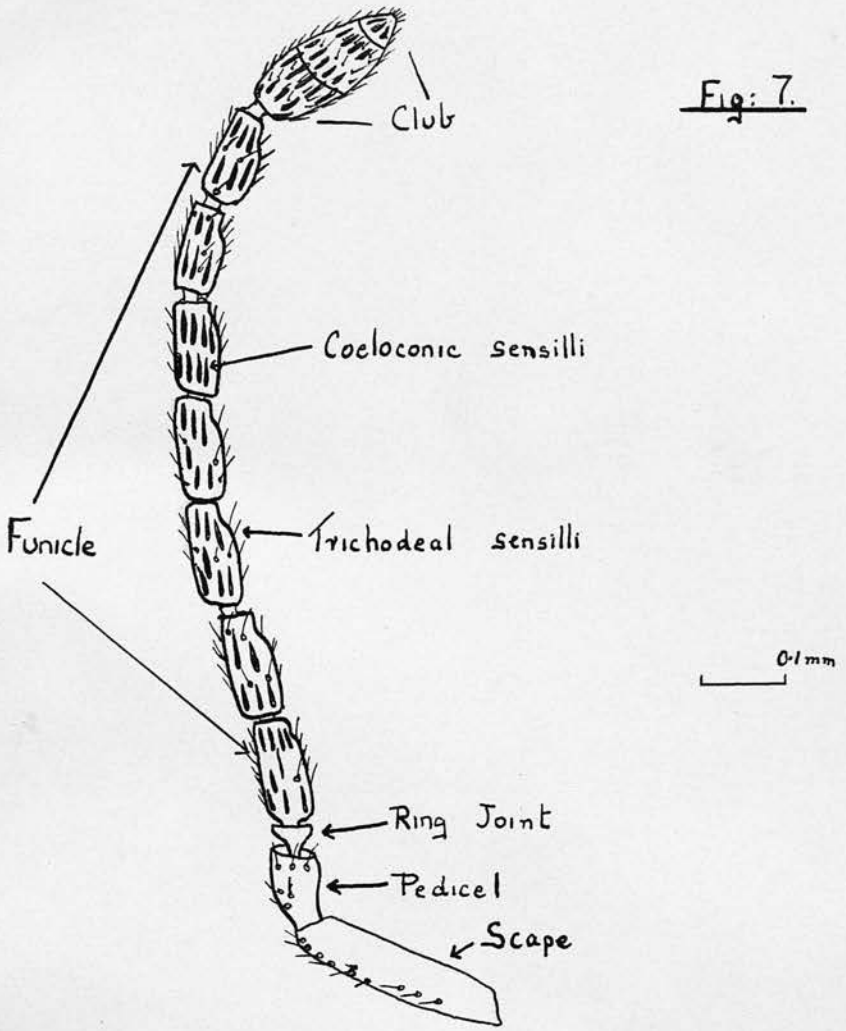
The maxillae consist of a basal, chitinized cardo for articulation with the wall of the head capsule. Distally the cardo is attached to a flattened stipes which bears a few setae on its outer surface. As previously mentioned the palp appears to arise from the stipes as a palpifer is indistinguishable. The maxillary palp consists of four segments with the terminal joint, the largest, bearing fourteen or fifteen setae.

The galea is a thickly chitinized structure, slightly domed so as to have a convex outer surface (bearing many fine hairs and spines anteriorly. Covering the concave, inner face is a delicate membrane, which apparently represents the lacinia, and shows a fine reticulation.

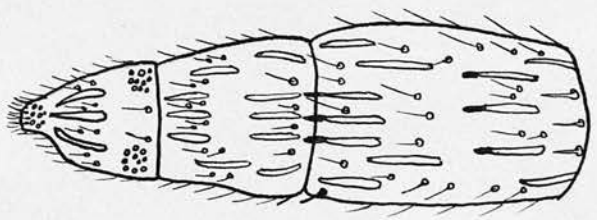
The Antennae (Fig. 7)

The/

Fig: 7.



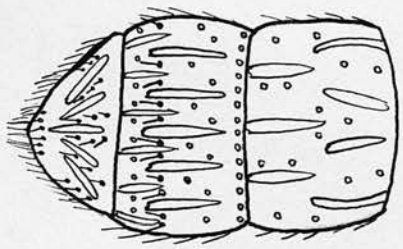
ANTENNA OF ♀ M. spermotrophus



♀ M. spermotrophus

♂ M. spermotrophus

0·1m



♀ M. dorsalis.

Fig: 8.

ANTENNAL CLUBS

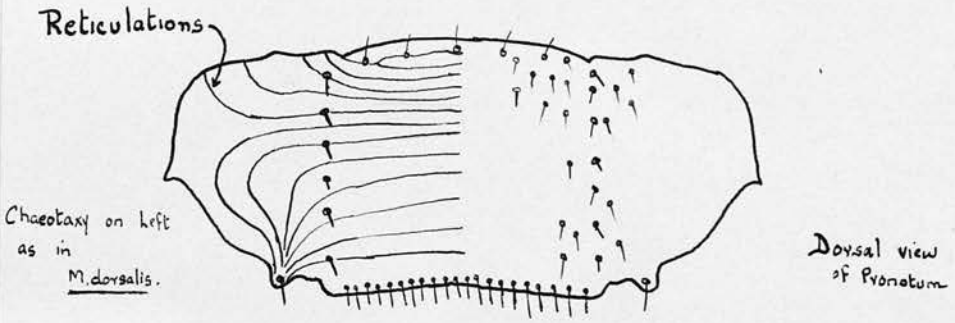
The antennae are geniculate as in all Chalcids and sexual differences occur. They consist of a scape, pedicel, ring-joint and seven segments comprising the funicle - at the apex of the antenna is a club composed of three fused segments. The total antennal length in the male is 1.38 mm. whilst in the female it is 1.61 mm. The greater length in the female is due to a longer scape and pedicel but in the male the terminal club is markedly longer probably associated with their active use in the copulation behaviour recorded later.

The organs, apart from the scape and pedicel, are clothed with sensory pits and setae. Contrary to the case of Harmolita where there is a greater number of sensory organs on the female antennae, the sexes exhibit no conspicuous difference in Megastigmus. However the terminal segment of the phytophagous male has definitely longer trichodeal sensilla than the phytophagous female whilst the latter has three small groups of pits, presumably sensory in nature, which are absent in the male. It is interesting to observe the greater concentration of coeloconic sensilla and the virtual replacement of trichodeal by pit sensilla in the parasitic species M. dorsalis (Fig. 8).

It would appear that these differences in sensory organs are correlated with a difference in habit. Reference to the discussion on copulation behaviour (p.55) seems to indicate that the male utilises his longer trichodeal sensilla on the apical antennal segment during his "display", when the rapidly oscillating antennae are brought into contact with the female antennae/

1·0mm

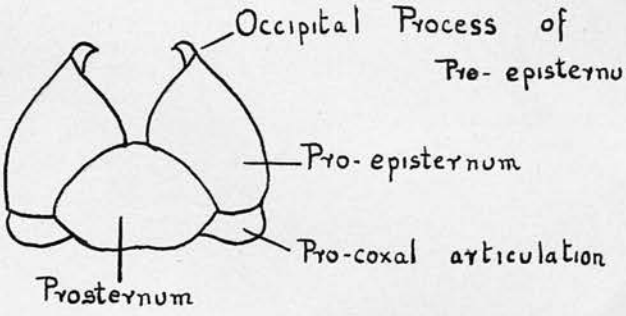
Fig: 9.



Prothorax of M.spermotrophus (Right)

0·5mm

Fig: 10.



Propectus (Ventral Aspect)

antennae by their extreme apices only. The presence of sensory pits in the female of both phytophagous and parasitic species may well be associated with the location of oviposition sites usually deep in plant tissue. This site is the embryo sac within the ovules of the seed, on the ovuliferous scales of conifers, in the case of M. pinus and M. spermotrophus and the larvae of the Cynipid inquiline Synergus in the galls of Cynipids in the case of M. dorsalis.

The Thorax

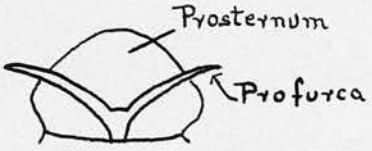
As in most Chalcids the thorax is highly specialized and owing to reduction, suppression and even addition of parts, the three fundamental metameric divisions are greatly obscured.

(1) The Prothorax.

The prothorax is characteristically separated from the other parts of the thorax as in other Hymenoptera. The Pronotum takes the form of an incomplete chitinized ring with a convex outer surface and overlaps the anterior portion of the mesothorax including the mesothoracic spiracles. The pronotum is covered by a series of minute folds running transversly dorsally, but becoming longitudinally arranged laterally (Fig. 9). The posterior band of backwardly directed setae is especially obvious. Fig. 9 illustrates the chaetaxy of M. dorsalis (parasitic form) on the left where the lateral setae are restricted to a single longitudinal line and M. spermotrophus on the right.

The pleuron of this segment (Fig. 10) consists entirely of the/

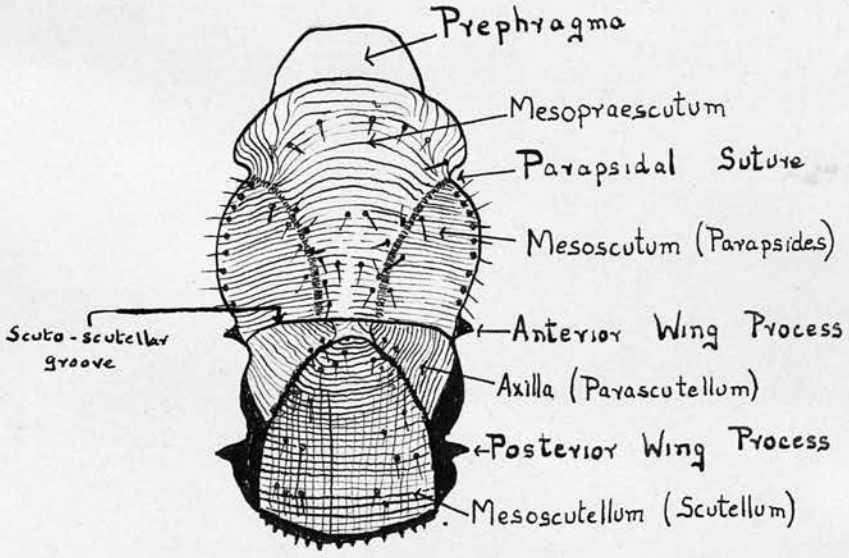
Fig: 11.



Propectus (Dorsal Aspect)

0·2 mm

Fig: 12.



Mesonotum of M. spermotrophus

the pro-episternum which is itself relatively larger than the prosternum. Anteriorly the pro-episterna terminate in a pair of processes which articulate with and support the head and are regarded by James as lateral cervical sclerites fused to the propleura.

The triangular prosternum carries the procoxal articulations posteriorly whilst dorsally it bears the profurca consisting of a diapophysis of two plate-like diverging processes (Fig. 11).

(2) The Mesothorax (Fig. 12)

The mesothorax is the largest segment in the thorax due to the necessity of accomodating the musculature of the forewing. Its dorsal region is separable into three parts. The two anterior plates represent the mesonotum whilst the third division, referred to by James as the postalar tergal plate or mesopostnotum. lies beneath the metathorax.

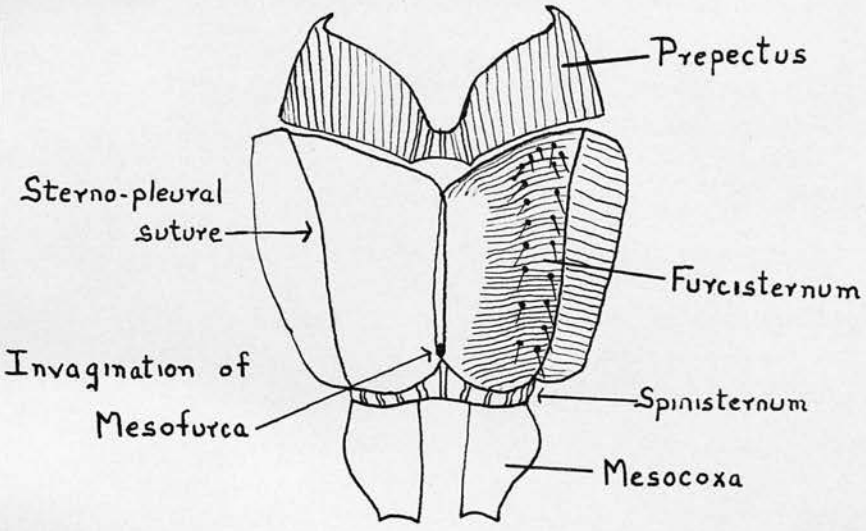
The anterior and posterior plates referred to above are separated along the well-marked scuto-scutellar groove which James, by an examination of the musculature, showed did not constitute a "dividing-line" in the thorax.

The most anterior of these plates is approximately triangular in shape and divided by the parapsidal sutures into three main areas. The middle area represents the praescutum which carries anteriorly a prephragma. The lateral sclerites are the parapsides and form the divided scutum of the mesothorax.

The reticulation of the praescutum is provided by a series of folds running transversely above, turning back towards the parapsidal/

Fig: 13.

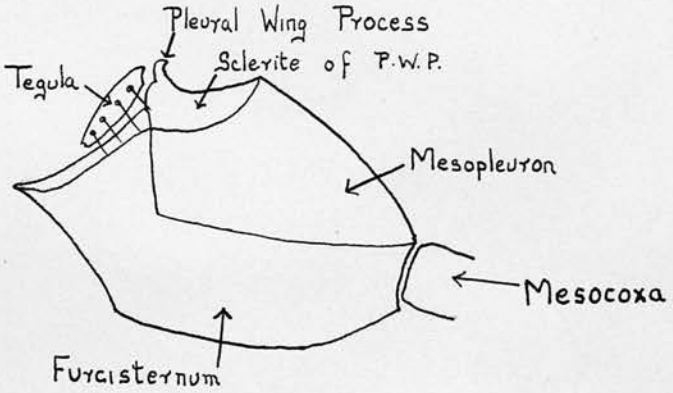
1·0 mm



VENTRAL VIEW OF MESOPLEURON & MESOSTERNUM.

1·0 mm

Fig: 14.



LATERAL VIEW OF MESOPLEURON

parapsidal sutures laterally (whilst the parapsides are covered by a series of folds running transversely). The setae on the parapsides are restricted to the region of the parapsidal suture and the lateral margin where they are especially long. The marginal arrangement of the setae on the praescutum leaves a dorsal area glabrous. At the posterior angles of the parapsides a fainter suture marks off small triangular sclerites named by James the sclerites of the anterior wing process.

The second anterior plate separated from the first by the scuto-scutellar groove is the scutellar area of the mesotergum. The large median area represents the meso-scutellum whilst the two lateral sclerites are themselves subdivided into the parascutella of James or axillae of Jalowcowy and a smaller posterior wing process.

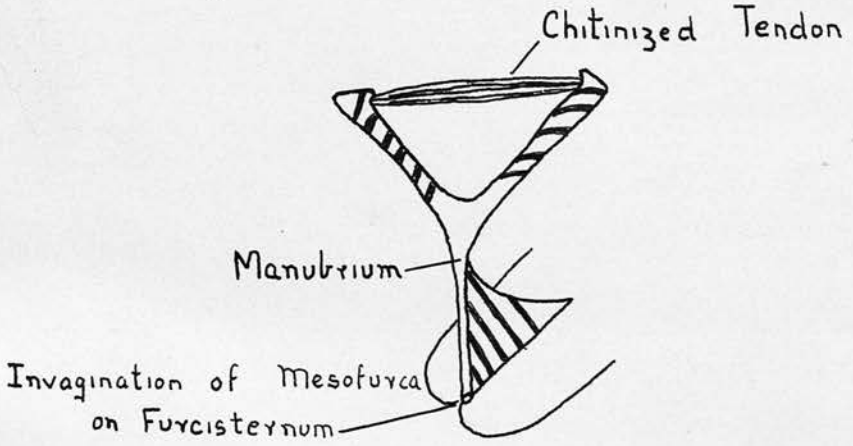
The axillae bear only two setae dorsally whilst the mesoscutellum carries its setae laterally so as to leave a dorsal area bare apart from the chequered system of ridges and furrows.

(2a) The Mesopleuron (Fig. 13)

Typically the pleuron of a thoracic segment is divided into two sclerites by an oblique suture - in this specialized form however the mesopleuron consists of a single plate, the pleural suture having entirely disappeared. Jalowcowy depicts and names an epimeron and episternum in this sclerite in M. kuntzei but there is no evidence of their occurrence in the species studied in this work. This mesopleuron is elaborately reticulated with a patchwork of ridges.

In/

Fig: 15



Mesofurca (Lateral)

In close proximity to the pleural process of the forewing is a small sclerite which has been referred to by various authors under the following names :- posterior basalare (Crampton), episternal parapterum (Snodgrass) and tegula (James). The tegulae in Megastigmus (Fig. 14) are elongate scale-like sclerites situated above or in front of the anterior wing processes. They have a dorsal convex surface which bears four setae whilst the concave lower surface rests on the sub-costal "scale".

(2b) The Prepectus (Fig. 13)

The pectus is a convenient term given by Snodgrass to the pleura and sternum of a thoracic segment. Snodgrass reserved the term prepectus for the Hymenopteran thorax only, but James regards it as homologous with the pre-episternum of Hopkins (in Dendroctonus Col.). In Megastigmus it is a plate in front of the mesopectus and is continuous across the mesosternum and mesopleura on each side.

(2c) The Mesosternum

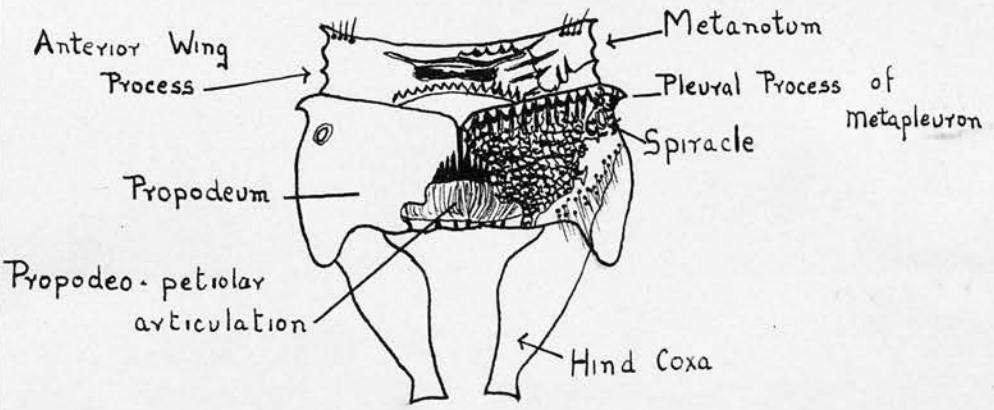
This region consists anteriorly of the prepectus behind which is a large plate, the furcisternum which carries the mesofurca dorsally. The lateral limits of the furcisternum are the conspicuous sterno-pleural sutures. The meso-coxal processes are borne on a narrow plate, the spinisternum which is elaborately ornamented by a series of longitudinal ridges. The furcisternum (a name based on Crampton's nomenclature) is covered with a delicate [redacted] of reticulations and bears two lateral rows of setae towards the sterno-pleural suture.

(2d) The Mesofurca (Fig. 15)

In/

Fig: 16.

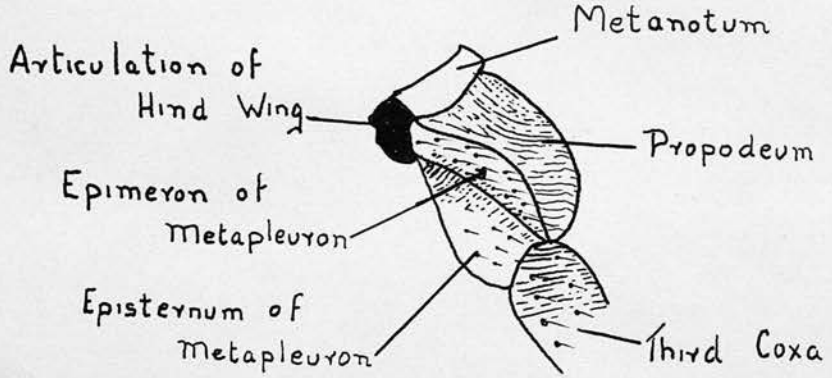
1·0 mm



Metanotum & Propodeum (Dorsal)

Fig: 17.

0·1 mm



Metapleuron

In Megastigmus this strongly developed apodeme appears in lateral view like a plate attached ventrally along the entire medium length of the furcisternum, its lateral arms connected together by a chitinous tendon forming an arch, beneath which the central nerve cord passes.

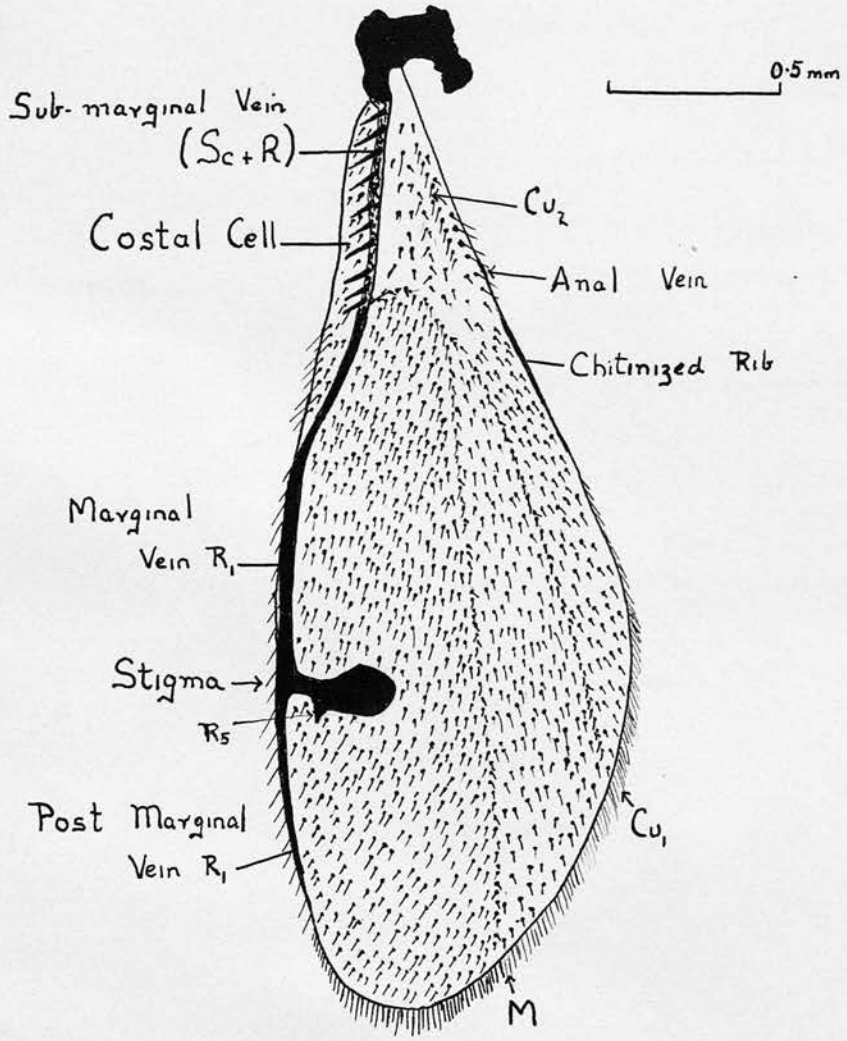
(3) The Metathorax (Fig. 16)

This segment is much reduced, appearing dorsally only as a narrow transverse band, the metanotum, immediately behind the meso-scutellum. Considerable confusion has arisen in the past when systematists referred to this segment as the postnotum of the mesothorax. This latter structure is in fact invaginated beneath the metanotum which is itself distinguished by the alar processes. The metanotum bears four setae towards each lateral margin.

(4) The Metapleura & Metasternum

There is no line of demarcation between the metapleuron and the propodeum but at the anterior angle is an anteriorly projecting structure, the pleural wing process of the hind-wing. The metasternum cannot be differentiated from the metapleuron or the propodeum at least externally, but James defined their limits in Harmolita by reference to the apodomes. There is, however, a definite groove in the metapleural area (Fig. 17) dorsal to which is an area bearing a number of small setae whilst ventrally few setae are present. It is presumable that this groove represents the pleural suture and that the dorsal area referred to is the epimeron of the metapleuron, the ventral area the episternum. Snodgrass has recognised that in the Hymenoptera/

Fig: 18.



FORE-WING of ♀ MEGASTIGMUS.

Hymenoptera it is possible to demonstrate a series of forms from the Tenthredinoidea, with a definite pleural suture demarcating an epimeron above and behind and episternum in front and below, to the Chalcidoidea where the pleural suture is obliterated.

(5) Metafurca

The metafurca is represented by two rod-like invaginations of the metasternum - they widen towards their apices and terminate at the apodemes of the metasternum mentioned above. The points of invagination of the metafurca on either side of the median line of the metasternum show, on the ventral surface, as pits.

(6) Propodeum

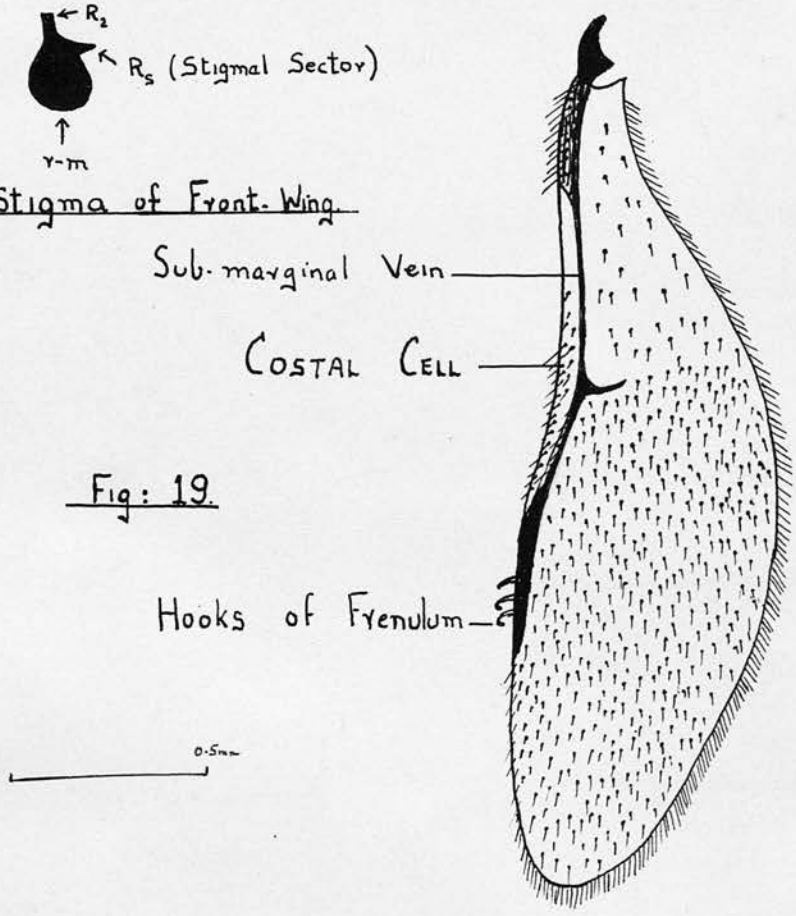
The propodeum is very closely fused with the thorax and is only distinct from the metanotum in dorsal view. Dorso-laterally it bears two spiracles which represent the first abdominal spiracles and are situated in smooth, unreticulated hollows.

The Wings

(1) The Fore-wings (Fig. 18)

The forewings of the female are longer than those of the male in Megastigmus spermotrophus, the length in the male being 3.0 mm. whilst the female wing measures 3.25 mm. the greatest width in male 1.20 mm. in female 1.25 mm. (Based on 20 individuals of each sex.)

The front margin of the wing is straight apart from a slight tendency to be concave between the wing-base and the point where it is joined by the marginal vein R_1. The rear margin is also straight and for some half of its middle length possesses a chitinous rib with which the hooks of the frenulum engage.



Stigma of Front. Wing.

Fig: 19.

Hind Wing of ♀

engage. The markedly rounded apical border is covered with fine hairs as are the upper and lower surfaces of the whole wing.

In common with other Chalcidoids, Megastigmus exhibits an extreme venational reduction but as Burks (1938) has pointed out the macrotrichia on the wing surface are often arranged in rows which are useful in tracing out the paths of obsolete veins. From Burks' study based on a long series of specimens from the group it is apparent that the costal vein is represented by the anterior margin of the wing, from the base to the beginning of the marginal vein. Immediately posterior to C is the sub-marginal vein, a product of the fusion of Sc and R. The marginal and post-marginal vein represent R_1, for near the termination of C there is in some forms a slight break which represents the end of Sc.

The stigmal vein is the second radial crossvein which leads into the "stigmal club", probably an r-m crossvein, whose "beak" or stigmal sector of Milliron is homologous with the R_5.

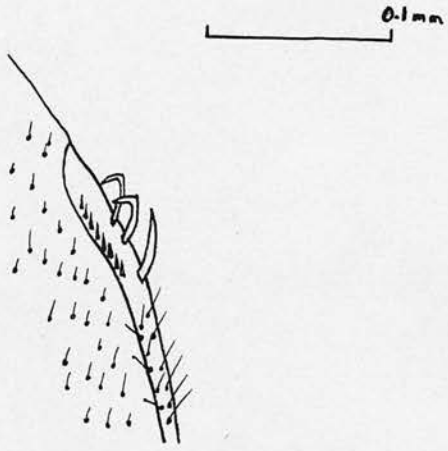
Studying the course of those macrotrichia which appear to be arranged in definite lines it is possible, by reference to Burks' series of illustrations, to define the M, Cu_1, Cu_2 and even part of a rudimentary Anal vein. (Fig. 18).

It is upon the shape, size, and inclination of the stigmal club that specific determinations of members of this genus are largely based.

(2) The Hind Wings (Fig. 19)

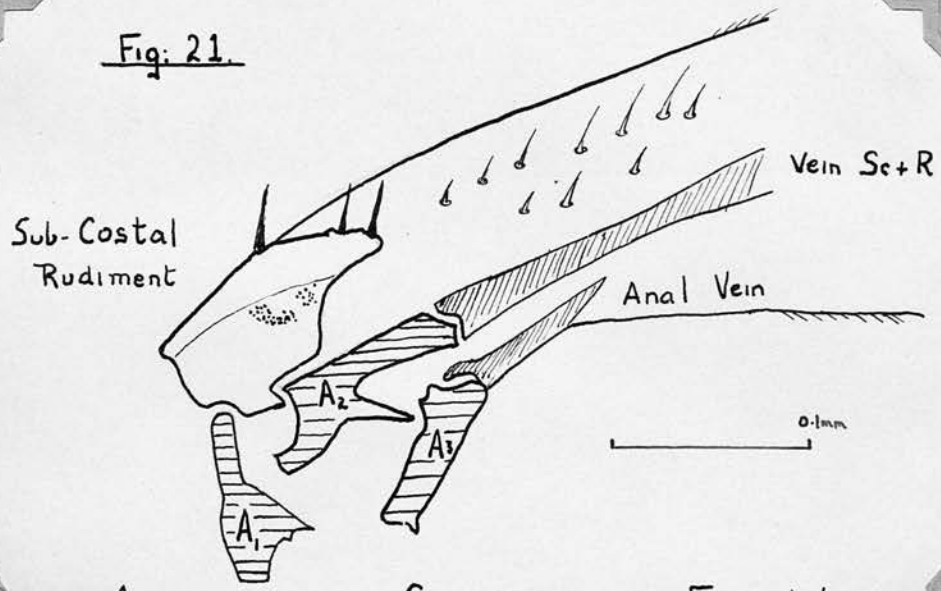
Once again a sexual difference in wing size is evident, the length/

Fig: 20.



Frenulum

Fig: 21.



ARTICULATORY SCLERITES OF FORE-WING.

length of a hind wing in the female being 2.65 mm. in the male 2.35 mm.

A fringe of fine hairs covers the posterior wing margin right around to the anterior margin. The sub-marginal vein, as in the forewing, encloses a Costal Cell behind the anterior edge of the wing but it is much shorter than in the forewing. Whilst the post-marginal and stigmal veins are absent. Wherever the veins possess setae they are considerably longer than those on the general wing surface.

The frenulum (Fig. 20) is a structure at the distal end of the sub-marginal vein consisting of strongly chitinized hooks, three in the female and four in the male except in Megastigmus dorsalis where the male has only three hooks. Usually two of the hooks are much more bent than the others. Posterior to this hook is a line of stout setae, absent in Harmolita, which, with the hooks serve to hold the chitinized band on the hind edge of the forewing both from above and below.

The Articulatory Sclerites of the Wing Bases.

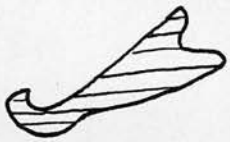
These sclerites serve to hinge the wings to the fulcral points of the thorax-anterior, posterior and pleural wing processes. Various muscles are also inserted therein.

(1) Articulatory Sclerites of Fore-Wing (Fig. 21)

There are three of these sclerites - the first (A_1) with a long curved neck which fits into a notch on the sub-costal rudiment - it also articulates with A_2 and the anterior wing process.

The /

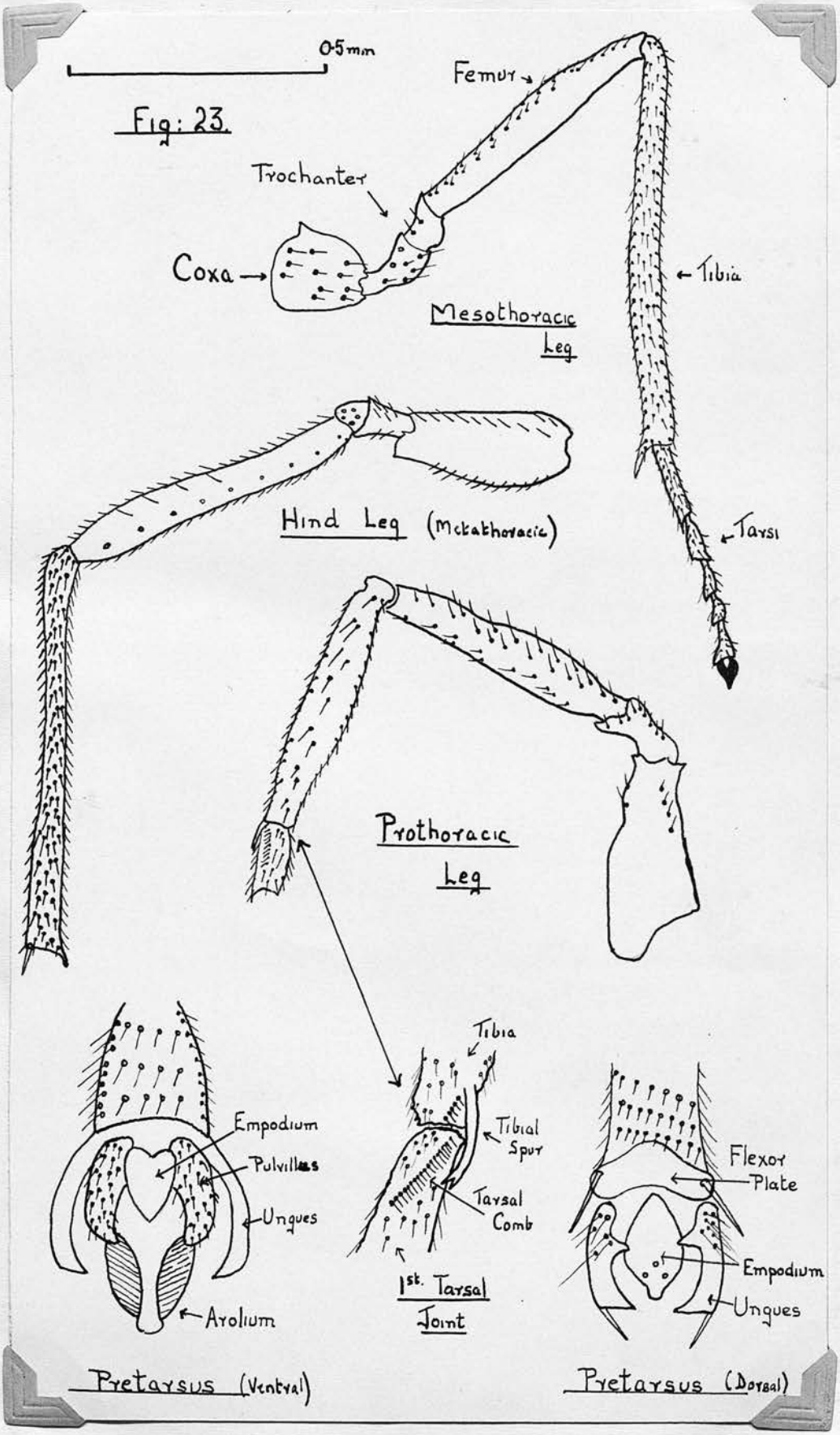
Fig: 22.



0·1mm

Articulation of Hind-Wing - Sclerite A2.

Scale


0·5 mm
Fig: 23.
Femur
Trochanter
Coxa
Tibia
Mesothoracic Leg
Hind Leg (Metathoracic)
Tarsi
Prothoracic Leg
Tibia
Empodium
Pulvilles
Ungues
Tibial Spur
Tarsal Comb
Arolium
1st. Tarsal Joint
Flexor Plate
Empodium
Ungues
Pretarsus (Ventral)
Pretarsus (Dorsal)

The second articulatory sclerite (A_2) is of a most irregular shape, articulates with the fork of the submarginal vein, A_1 and A_3.

The third sclerite is an elongate structure articulating with the posterior wing process and the rudiments of the anal vein.

(2) Articulatory Sclerites of Hind-Wing.

As in the fore-wing there are three of these sclerites but they are much smaller and excepting the second sclerite of the same general shape. They all articulate with the same sclerites and processes mentioned above.

The second articulatory sclerite of the hind-wing has noticeably shorter arms and a smaller neck than its homologous structure at the base of the fore-wing (Fig. 22).

The Legs (Fig. 23)

(1) Prothoracic Legs

The Coxae of these limbs are provided with two lobes which articulate with the episternum and sternum. They carry a short row of stout setae distally whilst the rest of their surface is ornamented by a series of curved, parallel ridges. The trochanter is typically divided in the Chalcidoidea, but in Megastigmus the division is not easily discernible externally. The trochanter is not reticulated and bears numerous setae. The femur is as large as the coxa and trochanter combined and has a convex outer surface sparsely clothed with setae. The tibia, slightly more slender than the femur, carries a bifurcate tibial spur at its distal end. This calcar is stouter and longer/

longer than that borne on the meso and meta-tibiae. It appears to function, in conjunction with two straight rows of short stout bristles, situated, one on the tibia and a longer set on the first tarsal joint, in cleaning the antennae.

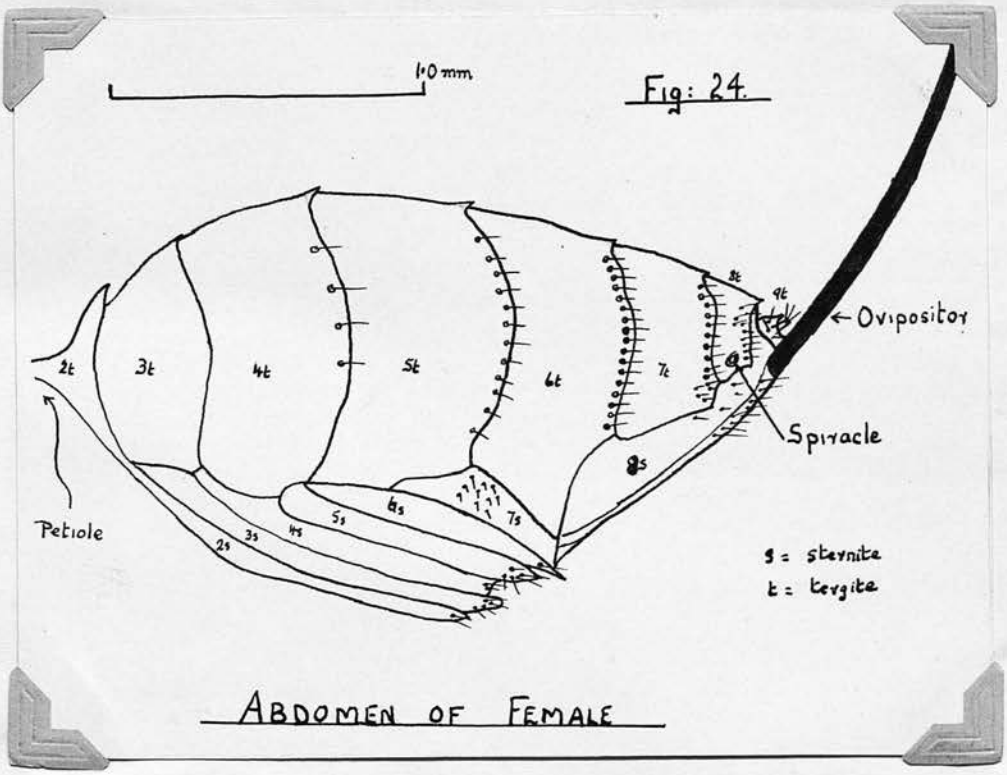
The tarsus consists of five joints, the first the longest -they decrease in length till the fourth but the fifth is nearly as long as the first. The joints are sub-cylindrical with their articulations oblique to the longitudinal axis of the limb and are densely covered with hairs, two of which, at the distal end of each joint, are much longer than the rest and considered by James to be of tactile function. At the distal end of the fifth tarsal joint the pretarsus presents a structure more complicated than that recorded by James in Harmolita. Normally this structure is obscured by the overlapping of the setose pulvilli and the pointed arolium, a partially chitinized membrane, which extends considerably beyond the bidentate ungues. Dissection of the pretarsus reveals the diamond-shaped empodium above which is a pad representing the flexor plate.

(2) Mesothoracic Legs.

The coxa is roughly heart-shaped and bears numerous long setae, it articulates with the posterior angles of the meso-sternum. The trochanter is apparently divided in this limb and bears sensillae as found by Grandi on Blastophaga . The rest of the leg segments follow the pattern of the fore-legs except that the tibial spurs are not forked and the comb device is absent.

(3) The Metathoracic Limbs

The/



ABDOMEN OF FEMALE

The hind legs are set so far back that they appear to articulate with the propodeum. The coxae are elongate cordate in appearance with two rounded articulatory processes. The trochanter is more obviously divided and bears a number of sensillae.

Workers on the Torymidae assume, in all the keys which I have consulted, that the hind tibiae carry two spurs, but in all the Megastigmus species examined in this work, only one is prominent so that care must be taken when assigning species to this group.

The Abdomen

This region of the body exhibits considerable differences in the two sexes, which will therefore be dealt with separately.

(1) The female abdomen (Fig. 24)

The female abdomen consists of ten segments. The first segment, or propodeum is firmly fused with the thorax and has already been described.

The second segment forms a narrow neck which joins the eight segments of the gaster to the propodeum. The second and third tergites are devoid of setae, but the fourth to eighth bear increasing numbers of setae on their posterior margins. The tergites increase in size from 2 - 5 and decrease from 6 - 10. The eighth tergite bears the second pair of abdominal spiracles. James, in his work on Harmolita, mentions a sensory plate on the ninth tergite said to consist of two circular depressions, on either side of the median line, from which/

which project four sensory spines with nerve attachments. He considers them to be characteristic structures of Chalcids, but no structure of this type is discernible in the Megastigmus species examined. The tenth tergite is very minute and bears an anal papilla.

The sternites 3 - 7 are markedly attenuated structures, backwardly projecting, and triangular in outline with the apical margins bearing a fringe of fine setae. All these sternites are chitinized apically but become membraneous proximally. The eigth sternite is divisible into two plates in Harmolita but this is not so in Megastigmus, where sternites 9 and 10 are absent and probably modified into parts of the ovipositor

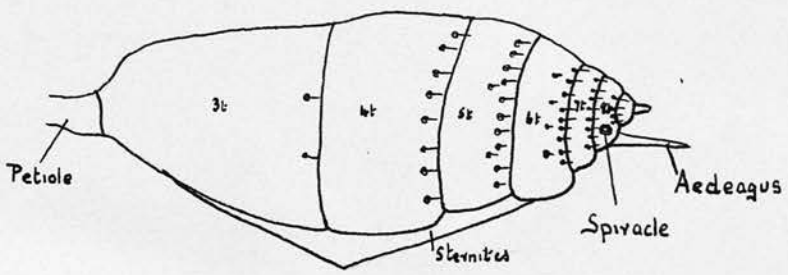
The ovipositor itself is composed of three pairs of gonapophyses.

The innermost pair of gonapophyses form the stylets of the ovipositor and consist of a pair of extremely fine needle-like structures with two barbs at their apex. The intermediate gonapophyses form a close sheath and are not easily separated, at their distal extremity they become blade-like and bear a number of tooth-like ridges.

The anterior end of each stylet expands to form a fulcral plate bearing two processes articulating with the third pair of gonapophyses referred to by Imms as the Inner plates. These plates in Harmolita and Blastophaga terminate in palp-like organs which are absent in Megastigmus where they take the form of outer sheaths to the ovipositor. Basally each plate

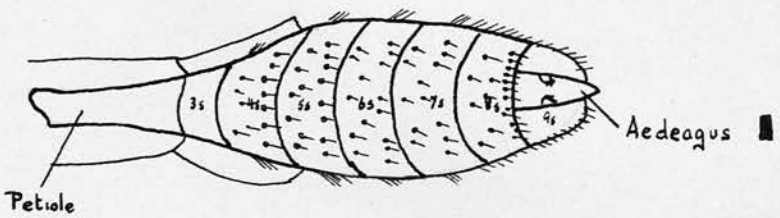
1·0mm

Fig: 26



ABDOMEN OF MALE (LATERAL)

S = sternite
t = tergite



ABDOMEN OF MALE (VENTRAL)

plate forms a chitinous condyle articulating with a process on the ovipositor sheaths and then expands posteriorly to form the falcate plates, supporting the areas formed by the arms of the sheath and stylets.

The outer plates of Imms or the quadrate plates of Snodgrass are two distinct plates articulating with the fulcral plates and which bear muscles whose contraction rotates the latter and so exerts the ovipositor.

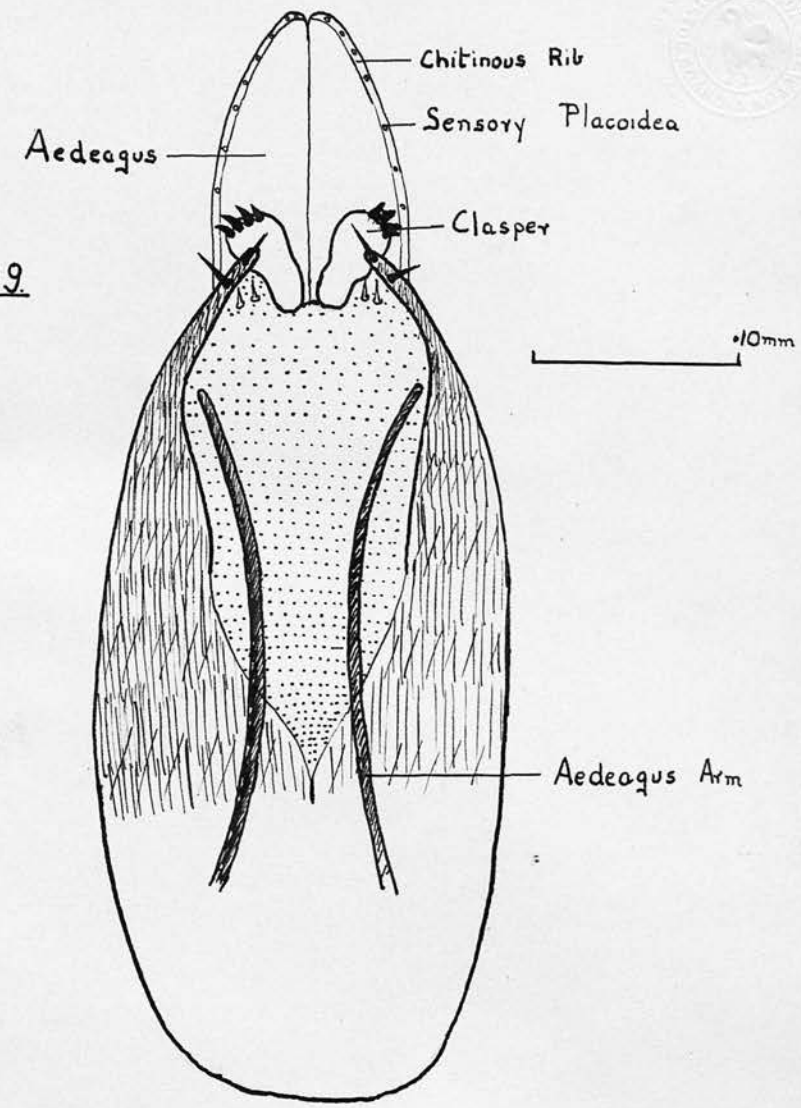
The most conspicuous part of the ovipositor is that referred to somewhat clumsily by Jalowcowy as valvulae aculei to which I shall refer as ovipositor valves. They normally enclose the stylets and sheath and take the form of long concave-convex valves, black in colour with a dense covering of thick setae being thickened and ridged in a curious manner (Fig. 25). They appear on dissection to be continuations of the inner plates or third pair of gonapophyses and probably replace the palp-like organs in Harmolita and Blastophaga.

The Male Abdomen (Fig. 26)

The male abdomen as well as being much smaller than the female possesses a markedly longer petiolar segment, this character is most evident in the ventral view. As in the female abdomen the tergites, sub-rectangular bands with curved lateral edges, increase in size from 3 - 5 and decrease from 6 - 10. The sternites are not carried forward anteriorly as in the female and so the tergites overlap their corresponding sternites, except the vestigial tenth tergite where the sternite is completely supressed. The eighth tergite bears a pair of spiracles and again no sensory plates occur on the ninth.

In/

Fig: 29.



♂ Genitalia of M. pinus.

In the ♂ genitalia the most conspicuous differences between the phytophagous and parasitic species were evident.

The aedeagus sheath is an incomplete chitinous cylinder, dorso-ventrally flattened, reaching in the contracted state from the anal papilla back to the fifth sternite. It is capable of protrusion beyond the apex of the abdomen for about half its length. Laterally, almost at the posterior end of the sheath, are two sensory spines whilst at the extreme tip are two elongate arms with two more sensory spines. These arms are capable of lateral motion and their function is probably to assist in keeping the organ in situ in copulation.

The claspers considered by most workers to be coxites of the ninth sternum take the form of curved organs; wider posteriorly, where they are armed with a varying number of strongly chitinized, curved, teeth.

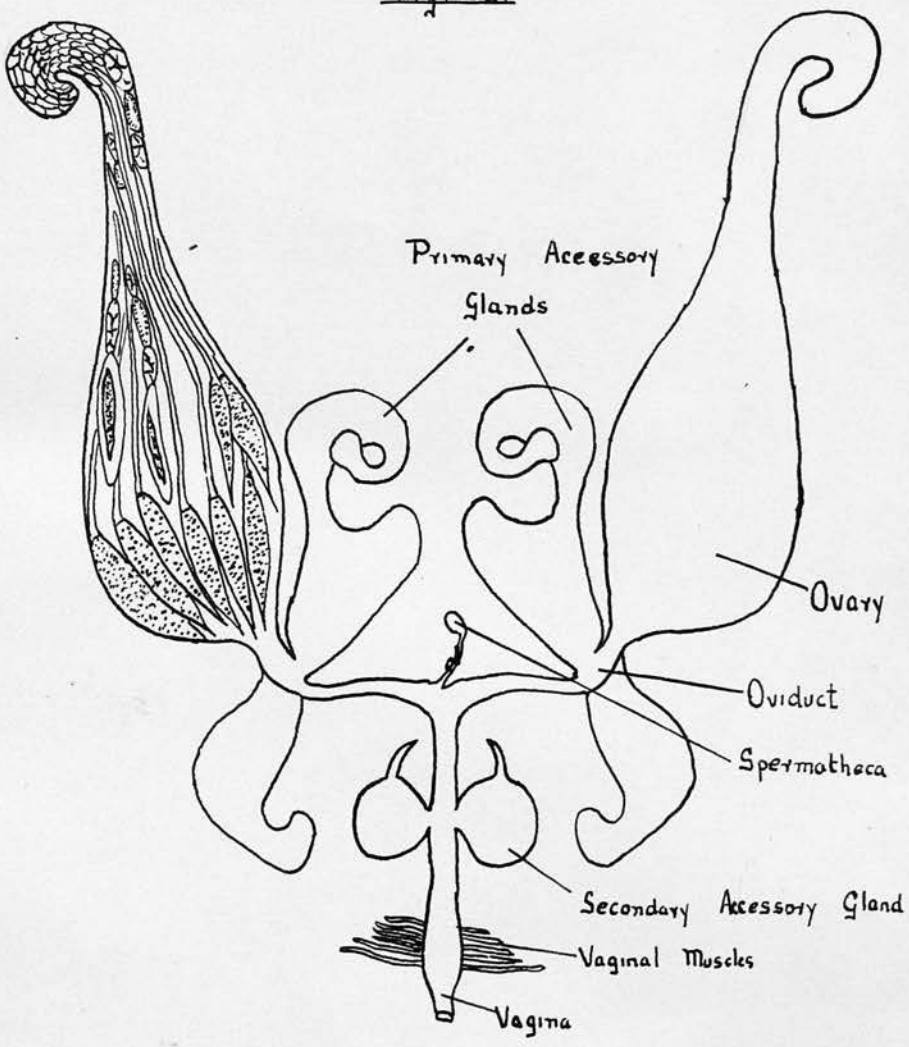
Within the sheath is a flattened aedaegus strengthened by a rib of chitin at its external borders along which a number of placoidal sensillae occur.

The claspers of M. dorsalis bear 2 teeth (Fig. 27)
" " " M. spermotrophus bear 3 " (Fig. 28)
" " " M. pinus bear 4 " (Fig. 29)

But in addition the aedaegus sheath of the parasitic species is noticeably longer and narrower than the phytophagous.

	Length	Breadth
M. dorsalis	.63 mm.	.09 mm.
M. spermotrophus	.45 mm.	.14 mm.
M. pinus	.51 mm.	.16 mm.

Fig: 31



FEMALE REPRODUCTIVE SYSTEM OF MEGASTIGMUS

Chapter II.

The Reproductive System

Section (a)

The Male Reproductive System

The reproductive system of the male (Fig. 30) consists of (1) the testes; (2) the vasa deferentia; (3) the vesiculae seminales; (4) the glandulae mucosae or accessory glands and (5) an unpaired ductus ejaculatorius, which opens externally behind the apex of the aedeagus.

The testes are much shrunken in the adult state and reach their maximum size only in the pupal phase whilst spermatogenesis is taking place. In freshly hatched males the vesiculae seminales are swollen with the mass of contained spermatozoa which appear as a whitish opaque fluid. The glandulae mucosae, elongate oval in shape, are attached by a short, obliquely running, duct to the proximal chamber of the seminal vesicles. The contents of these glands, more dense than that of the vesiculae seminales, are presumably the medium in which the sperms are transferred to the female.

Section (b)

The Female Reproductive System

The female generative organs (Fig. 31) consist of a pair of ovaries, each with an oviduct, which unite to form a common oviduct and vagina. There are two pairs of accessory glands and a spermatheca. At adulthood the ovaries occupy the greater part of the abdominal region.

Each of the ovaries consists of 14 ovarioles which adhere closely together/

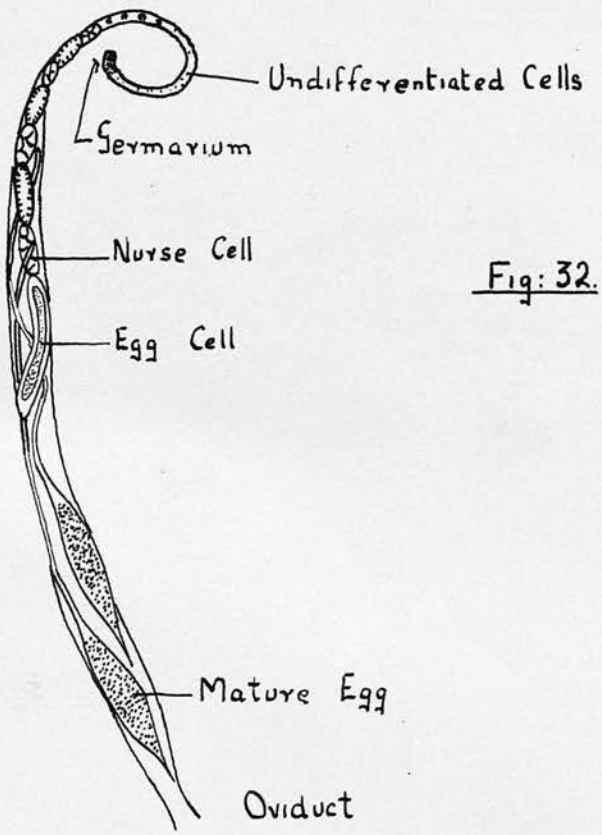
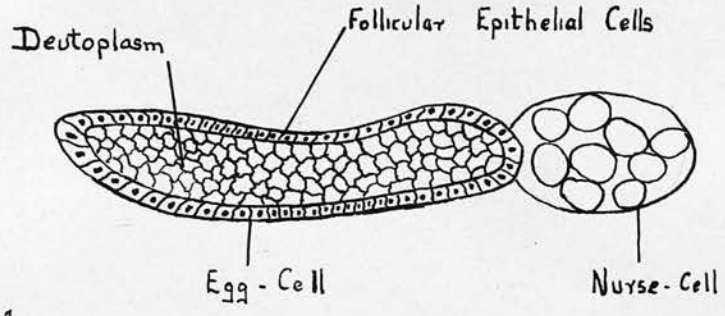


Fig: 32.

A Single Ovariole



1.

2.

3.

4.

5.

6.

Fig: 33.

STAGES IN OVULATION.

together and can only be dissected apart with care. Three regions can be distinguished in each ovariole (Fig. 32) - (1) a terminal chamber or germarium; (2) a zone marked by the alteration of egg-cells and groups of nurse-cells; and (3) a zone marked by the presence of mature or almost mature eggs. The terminal filament found in other Hymenoptera does not appear to be present. The germarium contains undifferentiated cells which, as development proceeds, will be transformed into egg and nurse-cells. In these polytrophic ovaries where egg and nurse-cells alternate with each other, and are each, in addition, situated in a separate slight dilation of the ovariole, the egg cells are surrounded by a ring of follicular epithelial cells. The ovariole wall is a delicate, transparent and very elastic membrane also lined with a folicular epithelium. As the egg-cells pass down the ovariole the germinal vesicle becomes obscured by yolk-cells as the deutoplasm forms and the follicular epithelium surrounding each egg-cell degenerates as it secretes the vitelline membrane. Finally, the follicular epithelium of the ovariole secretes the chorion, an extremely elastic and transparent "outer shell" which invests each egg. An interesting feature of ovulation in Megastigmus is the growth of the long anterior pedicel (Fig. 33) of the egg. The apical end of this pedicel (in a mature egg), while in situ in the ovariole, usually reaches back as far as Zone 2 or two-thirds of the total length of the egg tube. This stage is apparently only reached late in development. For after many dissections it seems established that the ova with attached nurse-cells pass more than half-way

down/

down the ovariole without any evidence of a pedicel. A constriction then forms which grows out into an elongate tube forceing the two bulbous ends apart. The lower bulb becomes the egg proper and contains the embryo whilst the upper bulb gradually deflates and becomes the attenuated anterior pedicel forceing its way back up the ovariole until fully extended.

When the adult female emerges from a seed there are one or two ripe eggs in each ovariole which indicates a total of from thirty to fifty eggs ready for oviposition within a short interval of time.

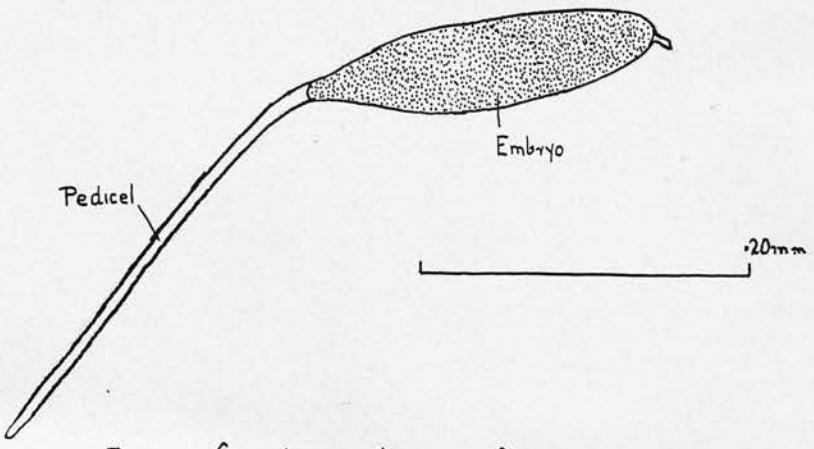
The terms Primary and Secondary Accessory Glands have been used for convenience and not from any established nomenclature. Grandi found only one pair of glands in Blastophaga but James depicted two pairs in Harmolita although both pairs were associated with the common oviduct. Further, neither of these glands found by James shows the characteristic shapes of those in Megastigmus (Fig. 31). Both are presumably associated with the production of fluids of a lubricating nature to assist the passage of the egg down the long ovipositor.

The spermatheca and the sinuous duct connecting it with the junction of the oviducts are heavily chitinized. It seems to store the sperms following copulation. The male cells pass down to fertilize each egg as it reaches the entrance of the common oviduct.

The vagina differs from the oviducts in having thicker, more muscular walls with numerous lateral muscles attached to the 7th abdominal sternite. Apically at is fixed to the ovipositor/

ovipositor sheath by attachment to the ventral surface of a V-shaped sclerite (Fig. 31).

Fig: 34.



Egg as found in situ in Ovary.

·30 mm

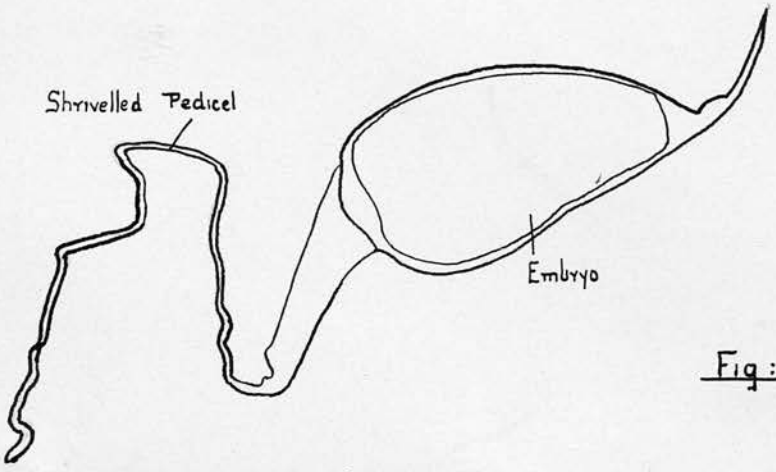


Fig: 35.

Egg as found in situ in D. Fir seed

Chapter III.

The Immature Stages of Megastigmus spermotrophus Wachtl.

Section (a)

The Egg (Figs. 34 & 35)

The egg of M. spermotrophus Wachtl. is composed of three parts - (1) a long narrow anterior pedicel, (that this long pedicel is anterior is shown by the position of the late embryo with its cephalic end directed towards the long pedicel); and (2) an elongate-oval body; and (3) a short spur-like posterior pedicel.

The average lengths of ten eggs after deposition:- Anterior pedicel .90 mm.; Body length .30 mm. and width .135 mm.; posterior pedicel .130 mm.

The ovarian egg, which is white and shining, has a smooth surface lacking ornamentation, and is considerably smaller as the following average measurements on ten eggs indicate.

Anterior pedicel .75 mm.; Body length .25 mm.; Body width .06 mm.; Posterior pedicel .008 mm.

These eggs are deposited within the jelly-like endosperm (♀ prothallus) of the seed but they are not laid in any constant position in relation to the archegonia; the anterior pedicel soon collapses and becomes a ribbon-like filament attached to the body of the egg.

Observations in the field indicate that the incubation period is relatively short and does not exceed five days, a similar/

similar period of not more than 4 - 5 days was claimed by Milliron (1949) for M. nigrovariegatus.

Just prior to hatching the space between the chorion and the embryo is filled with a colourless fluid through which the mandibles of the embryo are conspicuous. Eclosion has not been observed but Milliron claims that this is effected as a result of the outward movement of the mandibles rupturing the chorion.

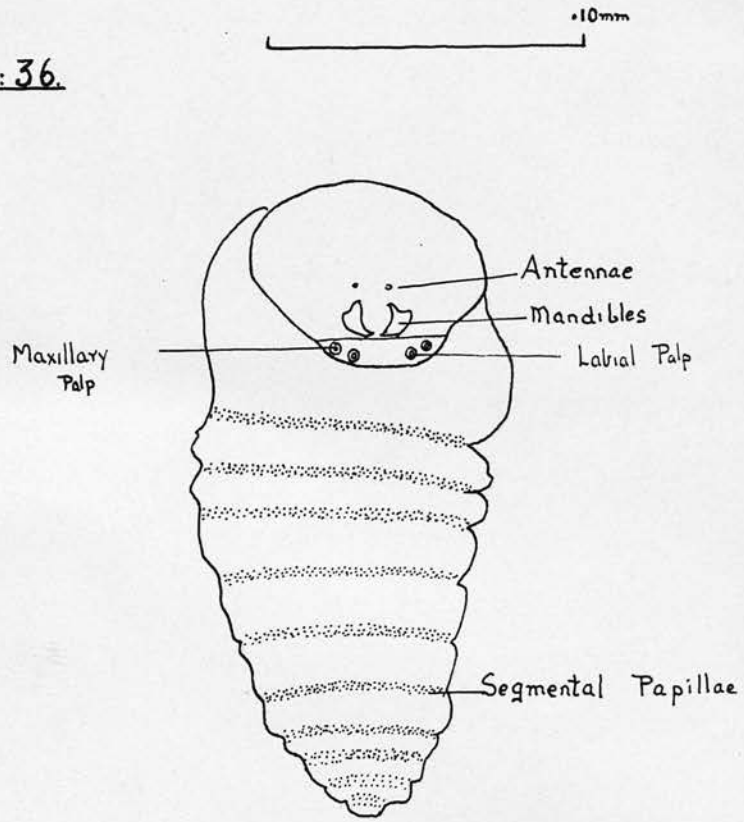
Section (b)

Larval Development and Larval Instars

As recorded later never more than one larva successfully develops within a single seed. When the egg hatches the seed embryo is still minute and the larva may be found anywhere within the jelly-like or almost liquid medium of the seed. Within a day or so of hatching however the larvae tend to migrate to the archegonia. As the seed develops the endosperm becomes firmer in constituency and is white in colour with the pale green cotyledons forming along the central axis. At this time the Megastigmus larva is usually located at the distal end of the seed from whence it commences to feed on the cotyledons. However the basal portion of the seed and the outer periphery of the endosperm remain intact until the 4th instar following which the entire contents of the seed are consumed apart from a white papery envelope immediately below the testa.

Larval development is extremely rapid and all the instars are passed through in the spring and early summer. Laidlaw (1931) reported that M. pinus was fully fed by September whilst/

Fig: 36.



1st. Instar Larva (Ventral)

whilst Balduf (1945) observed that larvae of M. nigrovariegatus were full grown in six weeks. In 1950 oviposition occurred in the first week of June (at Bedgebury, Kent) whilst the larvae were mature by the third week of July - a period of 6 - 7 weeks. 1951 was a later season for the cones but the Megastigmus were ovipositing at the same time although the larvae were not mature until the end of July. The duration of the earlier instars at Bedgebury during 1951 was - (i) 3 - 5 days, (ii) 5 - 10 days, (iii) 5 - 10 days and (iv) 7 - 10 days.

Descriptions of the instars are as observed in living material under the binocular microscope - the dimensions of the mandibles were obtained by mounting in gum-chloral and measuring the length from the tip to the base, between the condyles, as soon as cleared. The body lengths were observed on living specimens and as Milliron found with M. nigrovariegatus Ashmead are subject to considerable variations even within the same instar. By observing moults it is possible to obtain mounts of mandibles representing consecutive instars.

Five larval instars occur, these having been observed by studying the size and shape of the mandibles and the occurrence or otherwise of setae on the body. Measurements of the head-capsule were not used owing to the difficulty of avoiding distortion in mounting. Setae are best observed by rapid clearing in a solution of chloral hydrate dissolved in benzene.

First Instar (Fig. 36)

This instar possesses a head and 13 body segments. It is/

is minute, invisible to the naked eye, translucent with tendency to pale yellowish green in colder individuals. It is somewhat fusiform in shape, being broader anteriorly and tapering towards the posterior extremity. The head capsule only slightly narrower than the first thoracic segment, is hemispherical with a pair of blunt tubercles, only visible under very high magnifications, which indicate the subsequent location of the antennae. Each body segment bears on its anterior border two bands of very minute spines with occasional interspersed papillae forming a third row. All segments are devoid of setae and there is no evidence of a respiratory system.

Specimens of this instar range from .23 - .48 mm. in length.

The extremely sharp, pale golden and slightly curved mandibles overlap at the tips and range in length from .012 - .017 mm.

Unlike several other primary larvae of Chalcids, e.g. Microplectron fuscipennis Zett. the first instar larvae of Megastigmus lack sensillae on the labrum. The sensillae representing the maxillary and labial palpi are present as are another pair, within the hypostoma, common to other Chalcids.

Second Instar

The individuals of this stage are very similar to the first instar but the shape is less fusiform and as the thoracic segments have increased in width the head appears proportionately smaller. The individual body segments are more conspicuous than/

than in the earlier stages. Specimens are translucent, greyish white, except in the region of the alimentary tract which is pale yellowish green. Setae and anterior bands of spines are absent. In glycerine mounts the respiratory system shows as two lateral longitudinal trunks.

The mandibles are now quadridentate and triangular in outline with very sharp teeth. The tip is golden but the rest colourless. The size ranges from .025 - .041 mm.

The specimens range in length from .30 to .60 mm.

Third Instar

Specimens of this instar are less attenuated posteriorly and become more noticeably arched - they are greyish-white but the alimentary canal occupies a comparatively large area and is markedly yellowish green. The respiratory system is more advanced with the longitudinal tracheal trunks united anteriorly but not posteriorly. There are no setae or spiracles present.

The mandibles still quadridentate are heavily chitinized - the bases being pale amber with the tips heavily chitinized. The teeth are more closely set than in the previous instar. The mandibles range in size from .047 - .060 mm.

The specimens observed in this instar were from 0.5 - 1.5 mm. in length.

Fourth Instar

This instar is very like the preceding stage and is extremely hard to recognise except by reference to mandible measurements. The body is very strongly arched and cylindrical with/

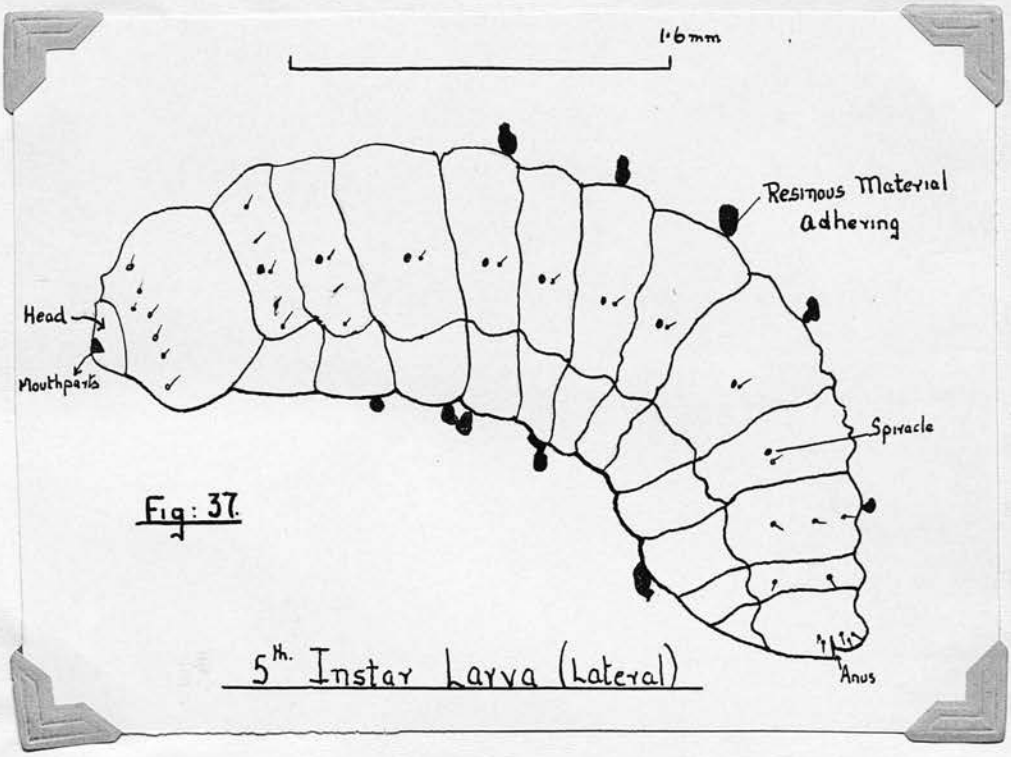


Fig: 37.

5th. Instar Larva (Lateral)

with little evidence of taper. The alimentary tract is longer and its contents tend to give the larva a pale green appearance. The respiratory system is well developed with the longitudinal tracheal trunks united posteriorly as well as anteriorly and numerous lateral branches passing out to the internal organs. In more advanced larvae of this instar the developing spiracular trunks can be seen. A depression at the hind end marks the position of the developing anus.

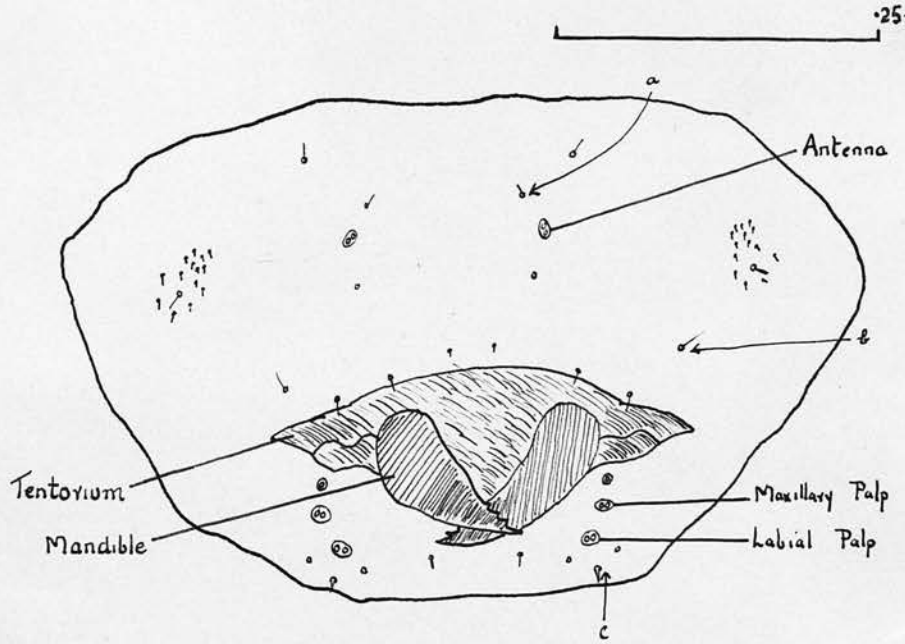
The sensilla of the next instar now appear in the labral region but setae are still absent.

The pale amber triangular mandibles vary in length from .070 - .085 mm., whilst specimens measuring from 1.00 - 2.4 mm. were found to belong to this instar.

Fifth Instar (Fig. 37)

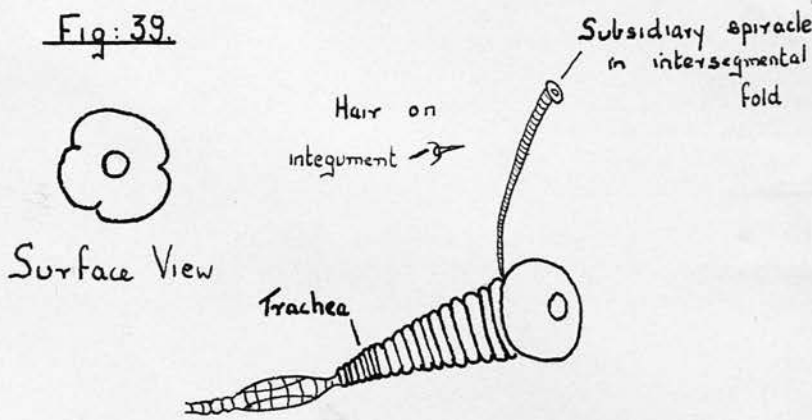
Fifth, final, instar larvae are white to dark grey in appearance according to the quantity of fat body which obscures the grey contents of the alimentary canal. As they reach full growth the body becomes strongly arched; the intersegmental folds are conspicuous as are other folds present laterally on the anterior segments. The head (Fig. 38) is now quite a rigid hemispherical capsule - the antennae being represented by a pair of sensilla each with two pits. The larger setae are fairly constant in position but the smaller ones depicted are not always present. The pairs above and between the antennae (a) outside and ventro-lateral to the antennae (b) and a pair ventral to the mandibles below the sensilla (c) are always present. The sensilla universally present are those representing/

Fig: 38.



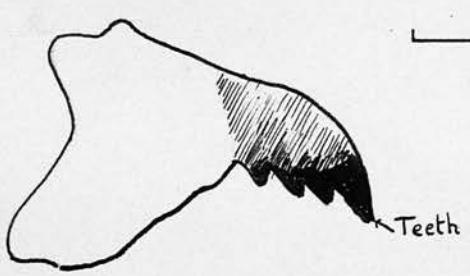
HEAD CAPSULE OF M. SPERMOTROPHUS.

Fig: 39.



ABDOMINAL SPIRACLE (Lateral)

Fig: 40.



Outer Surface View

MANDIBLE OF FIFTH INSTAR

representing the antennae, maxillary and labial palps, although in addition the maxillary and labial setae are sometimes replaced by placoidal sensillae.

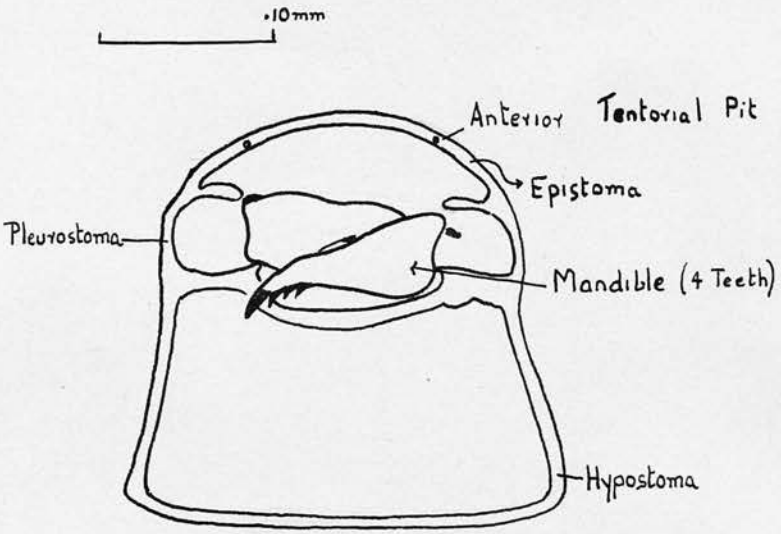
The quadridentate mandibles (Fig. 40) are bluntly toothed and heavily chitinized ranging in size from .095 - .116 mm.

Each thoracic segment carries a circle of setae, the first carries six setae on each side, the second five setae and the third three setae. These setae become progressively smaller posteriorly. The first seven abdominal segments carry a seta behind the spiracle. The ninth segment carries three pairs of setae, one pair latero-dorsal and two pairs latero-ventral in position, whilst the tenth segment carries three pairs of setae above and one pair below the anus.

Spiracles are present on thoracic segments II and III and abdominal segments I - VII. These spiracles are connected up with the two longitudinal trunks and from these junctions ramifying tracheae and tracheoles supply air to the body organs. All the spiracles are similar in size and shape except that those on the thoracic segments are slightly larger. The spiracles consists of a large almost spherical atrium with a circular aperture, below which the trachea diminishes in size gradually until it reaches the valve (which bears transverse and longitudinal striations). A most unusual feature is the minute tube leading from the inner surface of the atrium posteriorly to the surface in the first intersegmented fold behind the spiracle (Fig. 39).

The size range of this instar is from 1.8 - 4.0 mm.

A general study of chalcidoid larvae was published in 1924 by/



Cephalic Skeleton of 5th. Instar Larva

Fig: 41.

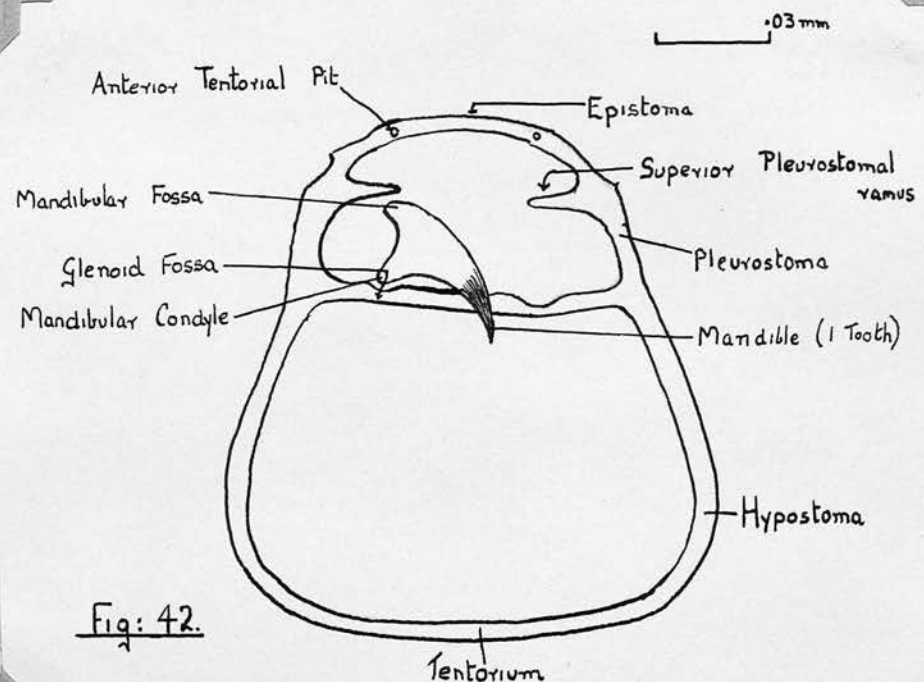


Fig: 42.

Cephalic Skeleton of 1st. Instar Larva

by Parker in which he recognised seven groups. This has since been increased to eight by Phillips (1927) working on Harmolita tritici (Fitch). E. Cameron (1939) working on two Chalcid genera Chrysocharis and Sphegigaster wrote more fully on Group II of Parker's classification, originally erected on Megastigmus dorsalis and with which all subsequent larval studies of the genus have agreed (e.g. Cameron 1939, Milliron 1949).

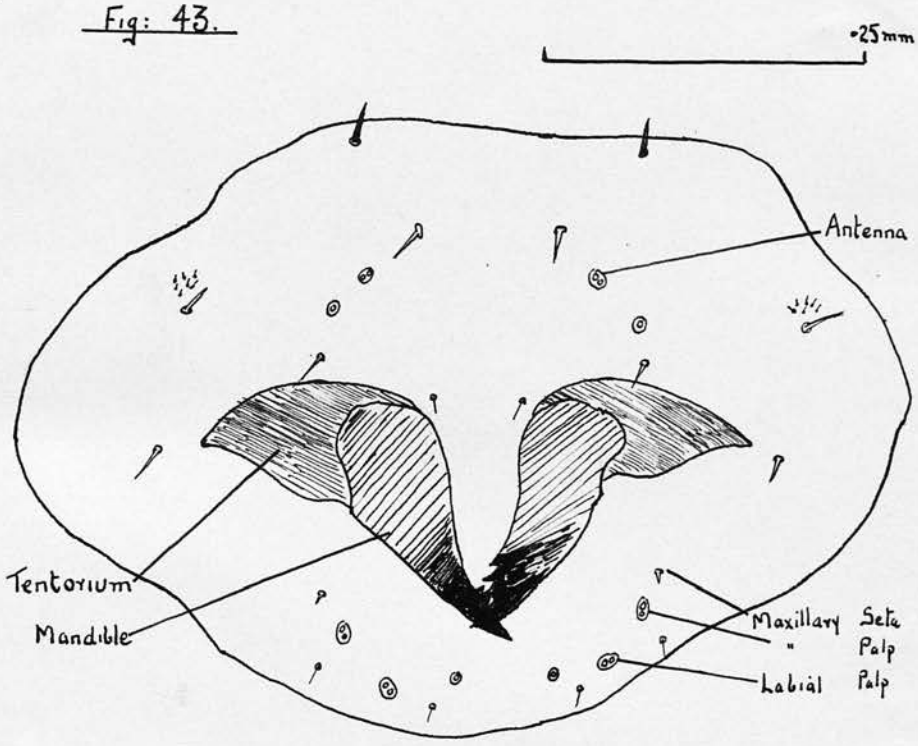
The external morphology of Chalcid larvae is similar in many respects to that of Ichneumonids and Braconids but the cephalic skeleton (Fig. 41 and 42) is more reduced, for example the stipital and maxillary scleromes, labiostipital sclerome and clypeal arch are wanting.

Parker's description of his Group II and Cameron's modification of it fits the primary larvae of Megastigmus spermotrophus and M. pinus in all except one important respect, e.g. the presence of spiracles.

"Head hemispherical, body fusiform consisting of thirteen segments. Antennae longer than broad. Tentorium very conspicuous with mandibles triangular and with a large lower condyle. The body segments are banded anteriorly with exceedingly minute spines. Spiracles are borne on segments 2, 4, 5 and 6."

In the mature larvae of the Megastigmus species examined the antennae are no longer well-developed and become replaced by sensorial pits, the tentorium, as in Sphegigaster, is still trapezoidal and the same criticism applied by Cameron to Parker's observations of the spiracles applies, in that the spiracles/

Fig: 43.



HEAD CAPSULE OF MEGASTIGMUS PINUS

spiracles, although open permanently, do possess a closing apparatus below the atrium.

Whilst this study serves to show that Parker's description of Group II in his classification of Chalcid larvae is within limits satisfactory and all species of Megastigmus, so far investigated, are readily referable to it; the respiratory differences between our phytophagous species and the parasite form (dorsalis) studied by Parker, indicate that a classification based upon the immature stages may lead to taxonomic divisions not evident from a study of adult characters alone. In this connection it would no doubt be of interest to investigate the structure of Megastigmus sp. B. (Nobel, 1940) which is said to be phytophagous in its early stages but later becomes an ecto-parasite.

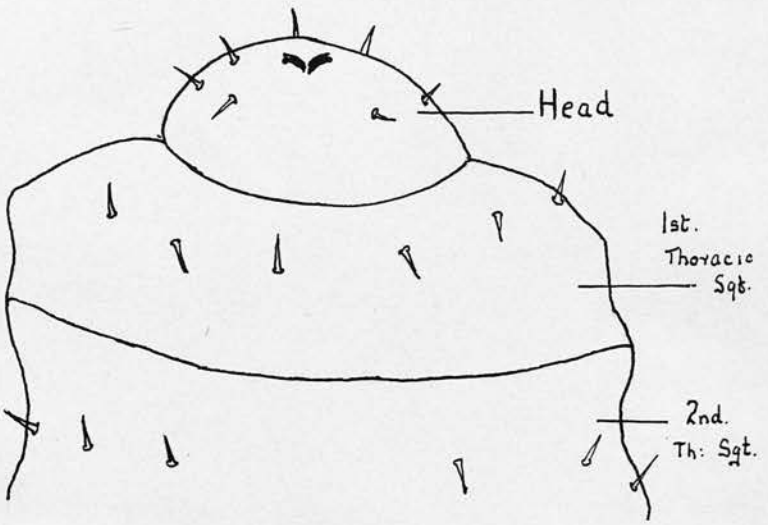
Section (c)

Comparison between larvae of M. spermotrophus and M. pinus.

References to Figures 38 and 43 shows that the head capsules of the larvae of these two species are strikingly similar. The only constant differences discovered concerns the replacement in M. spermotrophus of the maxillary setae/ of M. pinus, by a small sensillum and the fact that above the mouthparts M. spermotrophus has a line of eight setae - only six being present in the larva of M. pinus.

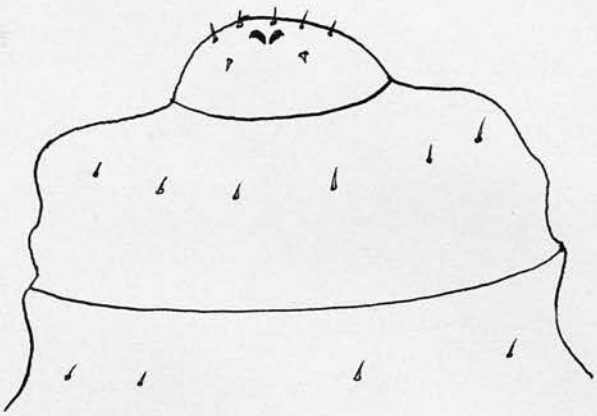
In life the two larvae are readily distinguished by the larger size of M. pinus, which when full-grown measures at least 4 mm. long. In addition M. pinus has markedly longer hairs on the head and thoracic segments. (Compared on same scale in Figs./

Fig: 44.



HEAD & THORACIC SGTS. OF M. PINUS

Fig: 45.



Head & Thoracic Sgts. of M. spermotrophus

Figs. 44 and 45).

Section (d)

Pupation and the Pupal period

Observations on this phase of development were made by dissecting out the fifth instar larvae from the seed and keeping them in a moist atmosphere at about 60°F.

After the larvae of Megastigmus have attained maturity in early July, they enter a state of diapause which requires an exposure to low temperature before terminating. Thus in the following late April and early May a proportion of the larval population will enter the prepupal phase - the remainder requiring a further one or two years in diapause. As recorded in the accounts of Rodzianko (1908), Escherich (1938) and Milliron (1949) indication of the onset of the prepupal phase is given by the expulsion of dark brown faecal pellets. Defaeciation is presumably delayed until this moment to reduce the dangers of fungal growth following a "fouling" of the micro-habitat within the seed. Escherich described these faeces as "little heaps of twisted string" and such indeed they are in M. brevicaudis Ratz., M. nigrovariegatus and M. pinus but M. spermotrophus extrudes a more liquid material which hardens into a series of pellets, which are not usually connected together into a string.

The body of the larva becomes more strongly arched and rapid internal changes begin, accompanied by a noticeable arching and increasing smoothness of the abdominal region which now appears somewhat reflexed at the caudal end. The thoracic region develops the conspicuous imaginal buds of the future

wings/

wings and legs and the adult head becomes visible, within the first thoracic segment of the larva, by reason of the orange-pink compound eyes. The average duration of the prepupal stage was three days.

A complete and detailed account of the pupa of Megastigmus is given by Milliron (1949).

Emergence of the pupa is effected by contractions of the pupal abdomen which causes a rupture of the larval integument behind the head capsule. Further abdominal contractions force the larval exuvia backwards until it remains as a crumpled mass at the distal end of the abdomen or ovipositor.

The newly formed exarate pupae of M. pinus are pure white apart from the pink eyes which gradually become more red until they are deep crimson with a dark rim, in both sexes, after five days. Pigmentation proceeds rather faster in the male pupae than the females - in the former the entire dorsal surface is black, at least subcutaneously, after seven days, but such pigmentation in the female, appears at first only on the thorax after eight days, and is complete on the dorsum in eleven days. Pigmentation resembling that of the adult is complete in the male pupa in nine days, in the ♀ in thirteen days.

In M. spermotrophus pigmentation appears first, in the pupae, on those areas which are black in the adult, after about seven days. By the eighth day hairs show on the wings, thorax and abdomen. On the eleventh day the body begins to assume a yellow-brown colouration and the wings appear almost black. Portions of the integument in both M. pinus and M. spermotrophus which/

which are yellow in the adult are greyish-white until 2 or 3 days prior to emergence.

Duration of the pupal stage in both species averages 13 days in the male, 17 days in the female.

Usually movement of the pupa is observed at least a day before emergence from the pupal theca - for beneath this theca the head and pronotum are capable of short movements as are the middle and hind legs. Coincident with this activity the theca becomes turgid especially in the thoracic region and eventually ruptures behind the head. The exuvia covering the thorax and abdomen is removed posteriorly towards the caudal end of the body exposing the wing pads, into which blood is then forced as they expand caudo-laterally. As the legs become free they are used extensively in peeling back the exuviae. The anterior portion of the pupal exuvia covering the head and antennae is removed by the front legs. The whole process lasting about one day. The adults remain inactive for a further day before excavating the circular exit-hole in the seed with their mandibles and during this time the wings become fully expanded and hardened for flight. It is interesting to observe that adults reared in tubes, after extraction from the seeds, only show a disposition to use their mandibles by biting the cork for about three days following emergence from the pupa.

Records of the duration of the pupal period of various species are given in the literature. Escherich (1938) states that the pupal period of the various forest species is three weeks, whilst Wolf & Zenck (1941) claim that the maximum period in M. spermotrophus is three weeks. Laidlaw gives the duration for/

for M. pinus as ♂ 19 days, ♀ 21 days. As shown elsewhere in this paper the period in M. pinus varies with the temperature:-

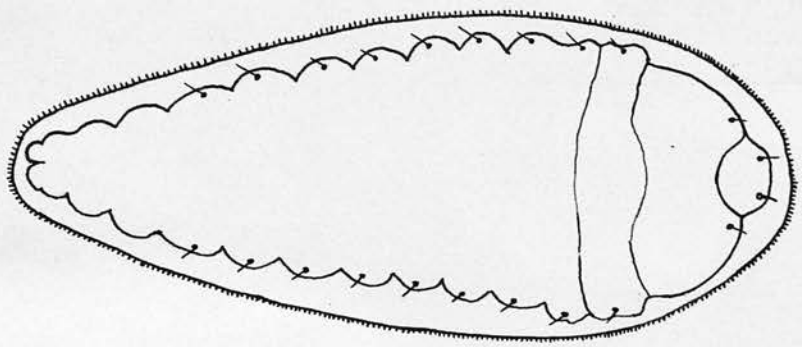
	77°	66°	60°
Pupal period in ♂♂	7	12	13
" " " ♀♀	10	14	17

In addition only Milliron in the literature distinguishes between the prepupal and pupal periods. Hence, field records at the average spring temperatures of Britain would indicate a pupal period of 4 - 5 weeks - a few days longer if the prepupal period is included. It is possible that increasing length of cold rest reduces the pupal period. In this connection Milliron's observation that full grown larvae of M. nigrovariegatus retarded into July, pupated in ♀ 12 days, ♂ 8 days, compared with earlier spring data of ♀ 15 days, ♂ 12 days is interesting.

Field records for M. nigrovariegatus by Balduf show that pupation began on April 24th and was complete by May 8th, emergence began on May 24th and lasted until June 20th. This date indicates that the average pupal period irrespective of sex was about 37 days.

Fig: 46.

·25 mm.



Egg of Amblymerus apicalis

Chapter IV.

The Parasite Complex.

Section (a)

Amblymerus apicalis. Thoms.

The Egg

The egg of this parasitic Pteromalid is elongate, ellipsoidal in shape (Fig. 46) and covered with a large number of short hairs so that it appears pitted in surface view. The dimensions are .46 - .48 mm. long by .22 mm. broad.

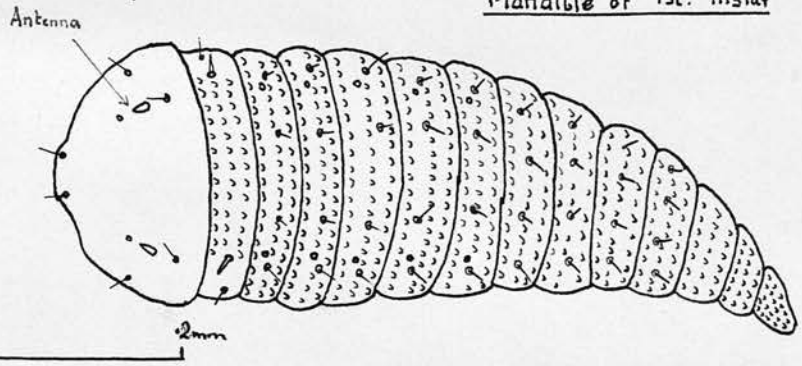
The embryo effects eclosion by splitting the chorion along one side.

These eggs are laid very late in the season (late October and early November in Ross-shire) which probably accounts for their discovery only recently. Seed collections for commercial and silvicultural purposes are normally made in September and early October so that Megastigmus larvae therein would not be parasitized. Previous attempts to study Megastigmus species have been conducted on such commercial seed stocks and so it is not surprising that parasites were unknown until a seed collection was made as late as December 1950.

The female places the egg within the testa of the seed but apparently makes no attempt to attach it to the Megastigmus larva, for having been dissected out with the larva, it will roll off at the slightest touch. However, as the host larva largely fills the lumen within the seed the egg is normally in contact with it. The length of the period prior to hatching is not easily determinable for the egg hatches almost/

Fig: 47.

Mandible of 1st. instar



FIRST INSTAR LARVA A. APICALIS.

almost immediately on being brought indoors at a temperature of + 58°F. At this temperature females, given seed infested with Megastigmus, laid eggs in September which hatched in four days.

Regular collections of cones throughout the winter and early spring revealed that these eggs, although laid in late October, do not hatch in the North of Scotland before the end of April.

Section (b)

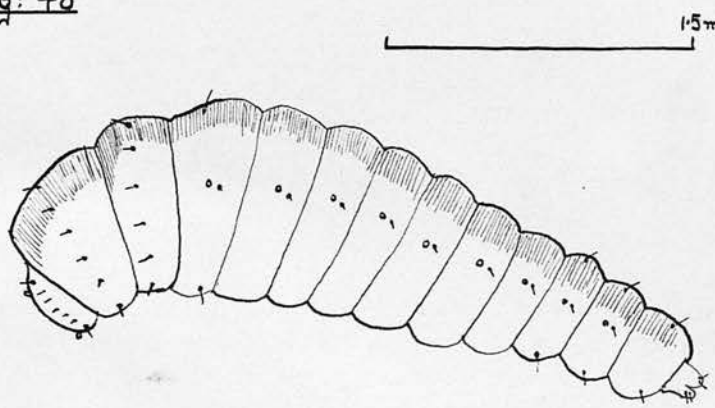
Larva

During its larval stages Amblymerus apicalis feeds as an ectoparasite upon the Megastigmus larva which it reduces to a minute fragment of cuticle. That the consumption of the host is total is emphasised by the appearance in the gut, of the parasite larva, of the characteristic "flower-like" resin "crystals" from the alimentary canal of the host.

When the parasite has totally consumed its host it bears a superficial resemblance to a mature Megastigmus larva but may be differentiated from it by the prominent antennae which are absent in Megastigmus. Other characters are the smoother dorsal surface of the abdominal segments - heavily folded in the host, and the marked contrast in the mandibles, which are elongate and unidentate in Amblymerus but approximately quadrate and quadridentate in Megastigmus.

The first instar larva of Amblymerus is whitish-translucent in colour with remarkably curved scimitar-like mandibles (Fig. 47) .019 mm. in length whilst the total length of the larva is about .6 mm. Each body segment is markedly tuberculate and segments 1 - 10 possess circles of setae. The head is very large/

Fig: 48



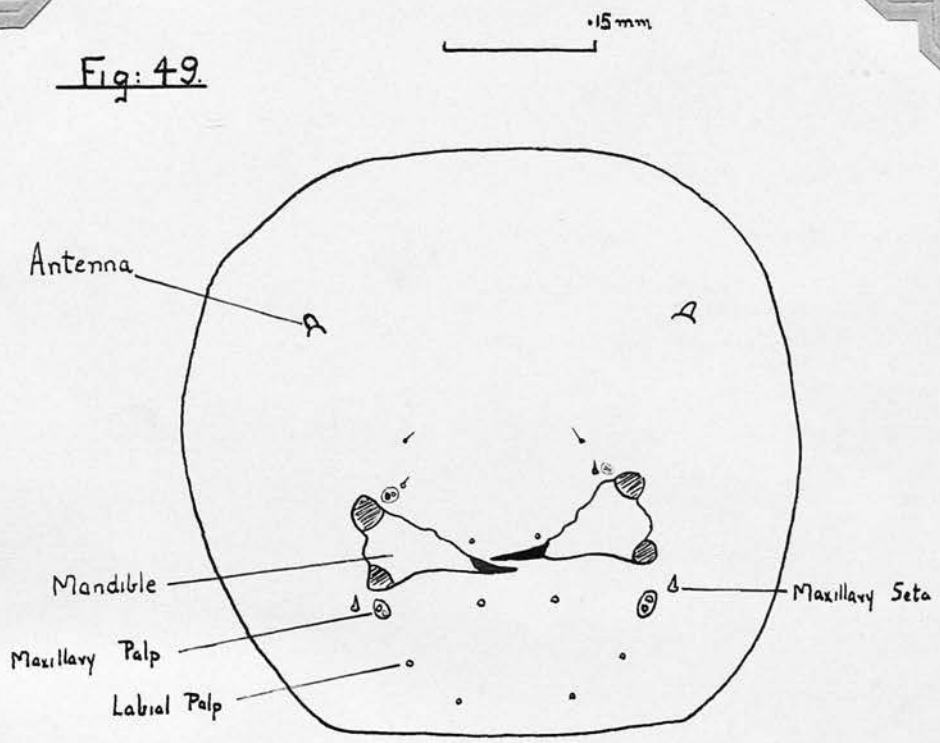
MATURE LARVA of AMBLYMERUS APICALIS

large relative to the 13 tapering body segments and bears noticable antennae. The young larva is very active and crawls about over the host often curling its attenuated abdomen up into the air. When feeding, all stages of the parasite larva bury their heads into the host tissues following superficial feeding. As material accumulates in the gut of the larva it becomes light-green in colour especially in the medial portion of the abdomen. Successive instars are characterized by a marked enlargement of the terminal abdominal segments so that the general body shape becomes "weevil-like" with a relatively small head still bearing its conspicuous antennae. The gut contents become a deeper greenish-yellow. The tracheal system with 9 pairs of spiracles and the longitudinal trunks become completely developed in the second instar. When mature the only hairs present are a ring around the pro- and meso-thorax with a single seta below each spiracle. The anus has 2 hairs above and below its orificeand segments 10, 11, 12 bear 2 lateral setae in addition to the spiracular setae (where present) - (Fig. 48).

As with Megastigmus the moulted skin of the previous instar is often found attached loosely to the larva and provides a most useful method of determining the number of larval instars by reference to the lengths of the mandibles.

Instar	Mandible Length	Total Body Length	Duration in Days
I	.019 mm.	0.6 mm.	2 - 4
II	.030 - .034 mm.	1.00 - 1.50 mm.	4 - 6
III	.039 - .042 mm.	1.70 - 2.20 mm.	5 - 10
IV	.06 - .064 mm.	2.4 - 2.7 mm.	5 - 10
V	.079 - .086 mm.	3.0 - 3.5 mm.	

Fig: 49.



HEAD CAPSULE AMBLYMERUS APICALIS

It is interesting to observe that the records of the mandible lengths for the different instars of both Amblymerus and Megastigmus show a definite tendency to observe Dyar's Law. Richards (1949) showed that growth proceeds at a regular rate so that the longer the instar the greater the amount of growth and hende that Dyar's original Rule only holds when the instars are of the same length. He further stated that a better fit was obtained if the data for the first instar was omitted (probably due to an initial period without growth) and that as linear measurements are more accurate than estimates of the duration of larval instars, the constant ratio attributed to Dyar was still suitable for checking experimental results.

For Amblymerus the ratios are :- 1.7, 1.3, 1.5 and 1.3

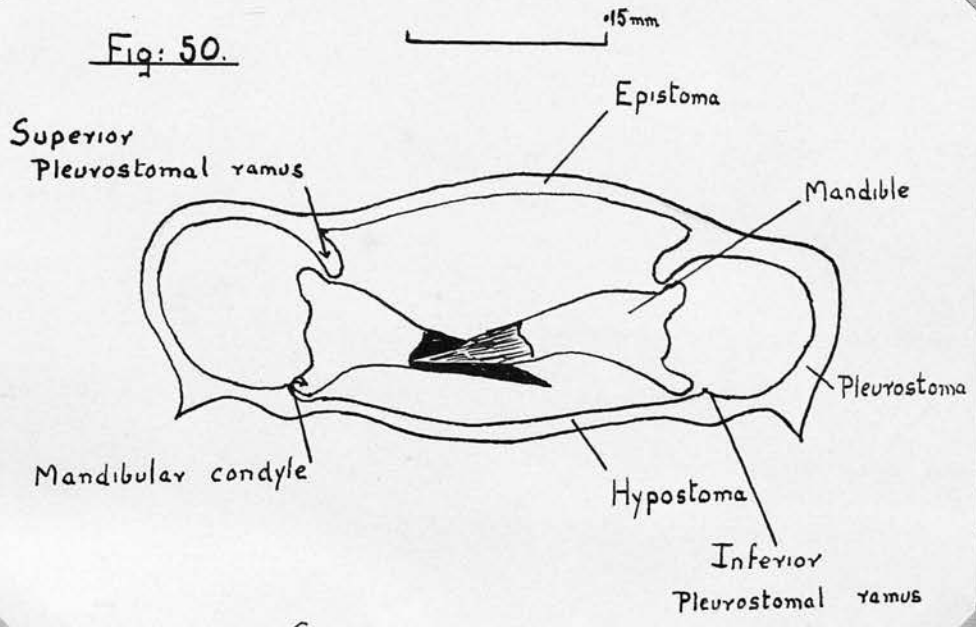
For Megastigmus " " " 1.3, 1.5, 1.4 and 1.4

Section (C)

Comparison between Head-Capsules of Mature Megastigmus and Amblymerus Larvae.

Reference to Figures 44 and 45 shows that the chaeotaxy of the Head Capsules of M. spermotrophus and M. pinus are practically identical although the setae are markedly longer in M. pinus. The principal difference between Megastigmus and Amblymerus (See Figs. 38 and 49) lies in the presence of antennae in the Pteromalid instead of two-pored pits in the Torymid. As mentioned earlier the mandibles are unidentate and needle-sharp in Amblymerus but larger and quadridentate in Megastigmus. The disposition of the setae and/or pits below the mandibular area are approximately the same but above the mandibles the arrangement/

Fig: 50.



CEPHALIC SKELETON OF MATURE A. APICALIS LARVA

arrangement of these setae is along converging arcs through the antennae in Megastigmus but in diverging arcs in Amblymerus. The parasite larva has only four setae above the mandibular area whereas Megastigmus has at least eight.

The shape of the cephalic skeleton (c.f. Figs. 41 and 50) is definitely distinct - the concavity of the epistoma in Amblymerus is less than in Megastigmus whilst the pleurostoma is much more curved in Amblymerus. The superior pleurostomal ramus has a downward curve in the skeleton of Amblymerus but it runs laterally and almost straight in Megastigmus. The hypostoma in Megastigmus tends to conform to the shape of a quadrilateral but in Amblymerus the figure represented is quite definitely six-sided.

Section (d)

Pupa

The pupa of Amblymerus is of the normal Hymenopterous exarate type. The head is directed ventrally with the tips of the mandibles opposed to the front coxae; the antennae reach the front tibiae. The front leg appears alongside the pronotum, the middle leg is placed adjacent to the thorax between the front femur and wing-pad. The proximal portion of hind femur is concealed but remainder of hind leg is visible, its tibiae extending to the abdominal venter. The front wing-pad extends caudo-ventrally, completely concealing the hind pad and parts of the legs indicated above.

Newly formed pupae are entirely white but gradually, within a few days, the compound eyes become distinctly pink. After/

Amblymerus pupa

Megastigmus (left)

Amblymerus (right).

After ten days the eyes are deep crimson.

The average pupal period of the male was 13.3 days, of the female 18.5 days. (data on 9 specimens).

Section (e)

The descriptions which follow were deemed necessary in view of the fact that neither of these three species has been described before in English. The system of nomenclature adopted is that used by A. B. Gahan (1942). I am indebted to Mr. Kerrich of the British Museum for the identifications. The individual descriptions are based on one specimen from the series whilst the lengths recorded are taken from all the specimens available.

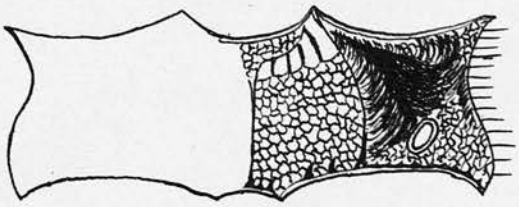
Description of A.? apicalis. Thoms.

Female

Head slightly broader than thorax, three times as broad as long at the middle, occiput distinctly concave: postocellar line equal to 2 times the occellocular line which is itself 3 times the diameter of an ocellus. Viewed from in front the head is broader than high (41 : 31), narrowed below the eyes, truncate at the mouth; malar space equal to not more than .375 of the eye-height; antennal scrobe shallow; eyes moderately large, ovate, bare; clypeus finely striated, rest of head nearly uniformly finely reticulate-punctate; right mandible distinctly quadridentate, left mandible tridentate; the inner tooth broad and very slightly concave at the apex; maxillary palpi 4-jointed. Antennae 13-jointed inserted a little below middle of head (25 : 20) on a line with the lower extremities of the eyes, distinctly/

0·25 mm.

Fig: 51.



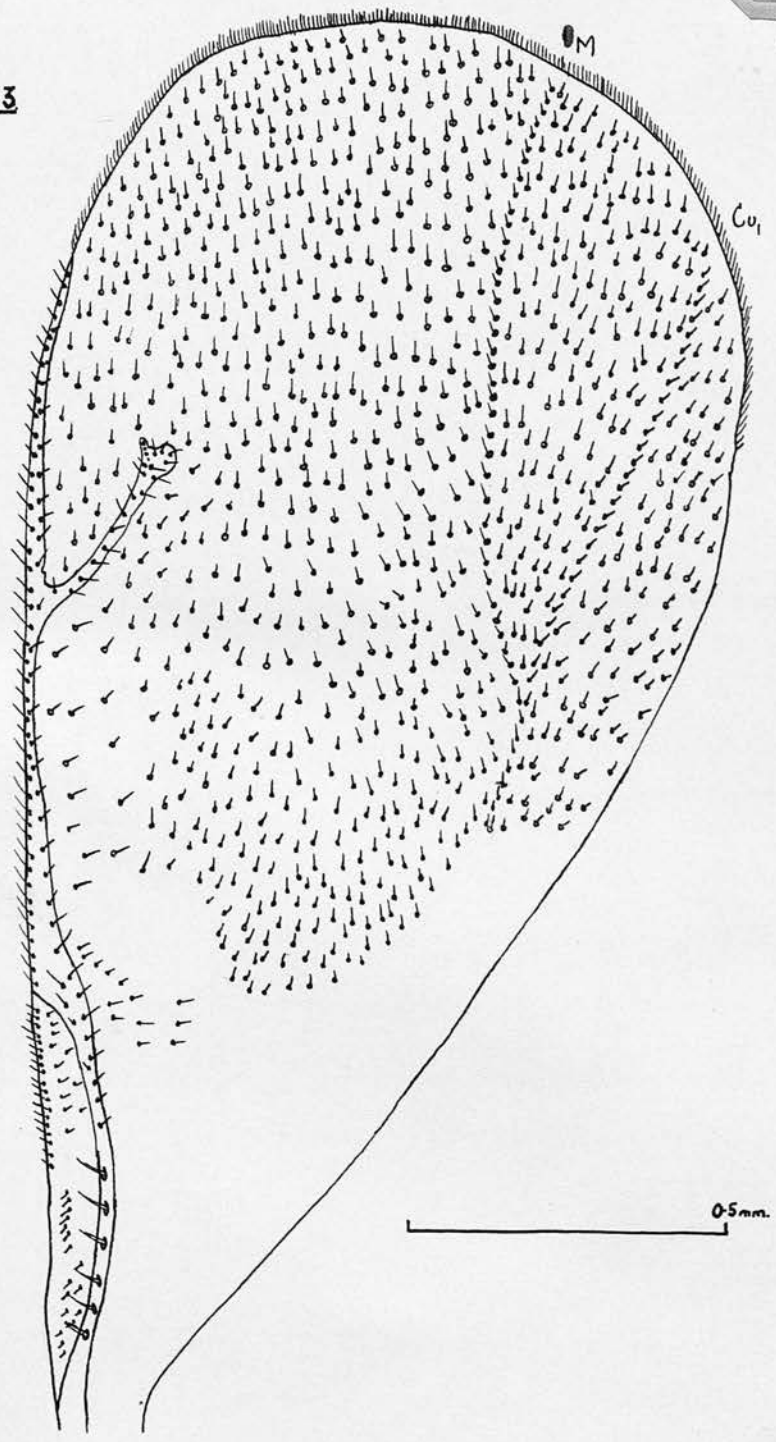
PROPODEUM OF AMBLYMERUS APICALIS

distinctly clavate; scape attaining the level of the top of the compound eyes, subcylindrical; pedicel a little more than twice as long as broad at apex, not quite as long as the ring joints plus the first funicle joint; 3 distinct ring joints, the first smallest; funicle 5-jointed, the joints successively increasing a little in width and decreasing very slightly in length; first funicle joint a little longer than broad, about equal to the 3 ring joints combined; 5th funicle a little broader than long; club distinctly thicker than funicle, ovate, a little longer than the two preceding funicle joints, funicle and club joints clothed with short inconspicuous hairs.

Thorax slightly more than $1\frac{1}{2}$ times as long as broad (65 : 45); pronotum short, the dorsal aspect transverse, a little narrower than the mesonotum, and nearly in the same horizontal plane as the mesoscutum, sculptured like mesoscutum, the anterior declivity nearly perpendicular; mesoscutum slightly convex, finely reticulate punctate at the sides but more coarsely punctate dorsally, about $1\frac{1}{2}$ times as long as broad (35 : 23), the parapsidal grooves weakly impressed anteriorly but effaced posteriorly; scutellum sculptured like mesoscutum especially posteriorly and anteriorly elsewhere a tendency to be finer, convex, distinctly shorter than mesoscutum , slightly longer than broad, axillae sculptured like lateral portions of scutellum and broadly separated; propodeum half as long as scutellum without a neck, with a median carina, lateral folds well developed and complete; spiracular sulci shallow; surface of propodeum between the folds distinctly wrinkled, laterally

from/

Fig: 53



FOREWING OF AMBLYMERUS APICALIS

from folds finely reticulate; spiracles circular; pleura sculptured like dorsum but upper portions of meso and metapleura very finely reticulate.

Legs normal, hind coxae more markedly reticulate than others.

Fore-wings about $2\frac{1}{2}$ times as long as broad (40 x 17) extending beyond apex of abdomen, bare basally; marginal cilia short; marginal vein a little longer than post-marginal (32 : 28) and twice as long as stigmal (32 :16). Abdomen ovate or conic-ovate, about as long as thorax and as broad or a little broader than thorax, smooth and polished dorsally at base, the apical tergites, all tergites laterad and the sternites with a faint reticulation. Ovipositor tip barely visible from above.

Head, thorax and abdomen a shining, metallic coppery green, antennal scape yellowish, rest of antenna yellowish below with dark brown marks dorsally, mandibles yellow-brown and brown at apices, rest of mouth parts pale yellow. Coxae concolorous with the thorax, rest of leg yellow testaceous except apical tarsal joint which is brown. Wings hyaline, venation testaceous. Compound eyes red with a black rim.

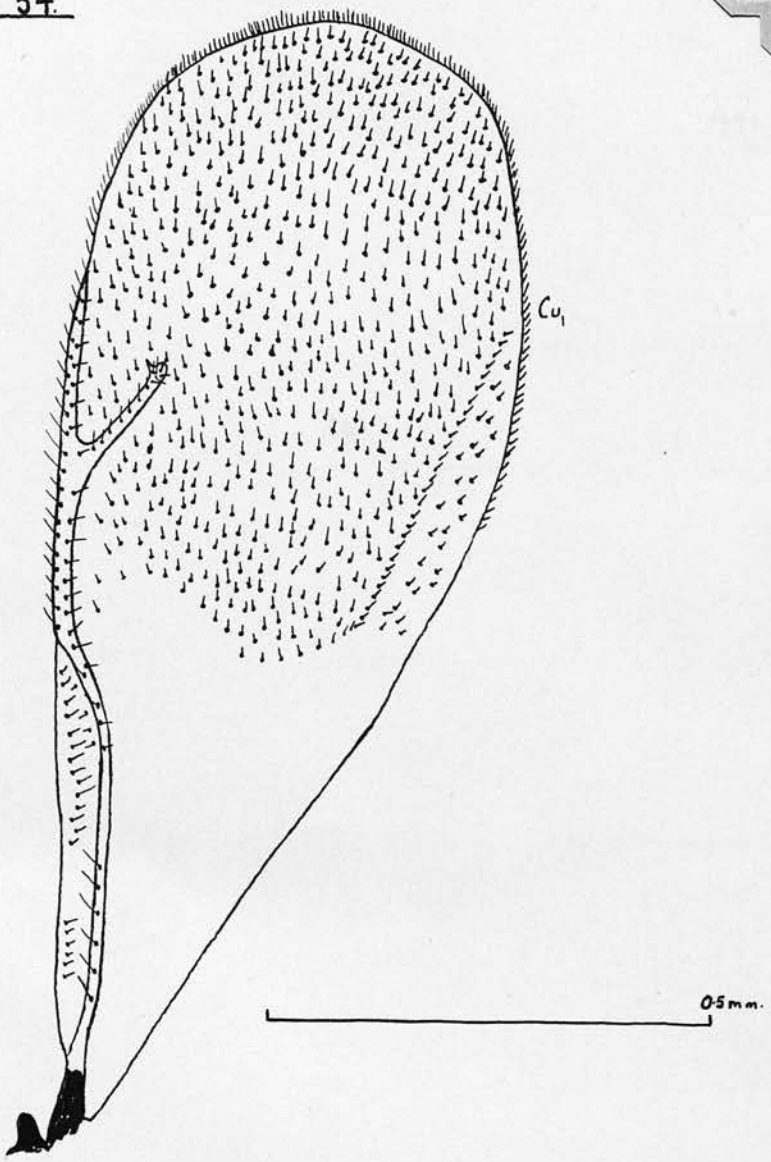
Length 2.5 - 3.7 mm.

Male

Description of proportions and sculpture of parts as for female excepting the proportions between the veins of the wings which are :- Marginal : postmarginal (21 : 20) and marginal : stigmal (21 : 16) and the fact that the antennae have 2 ring-joints and 6 funicle joints.

Colouration/

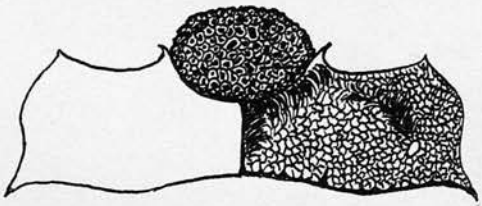
Fig: 54.



FOREWING OF TRICHOMALUS NR: SUNIDES

0·2 mm.

Fig: 52



PROPODEUM OF T. SPP. NEAR SUNIDES

Colouration of head and thorax as for female except antennae which are entirely yellow apart from the black club and dorsal surface of pedicel. Legs as in female.

Abdomen is coppery green, devoid of reticulation on the shining basal area of the second segment. Its most conspicuous feature is the bright yellow band encircling the body at the apex of the second abdominal segment, the whole of the third and fourth segments. This yellow ring is interrupted at the base of the fourth abdominal segments by brown marks on each side.

Length 2.5 - 3.0 mm.

Section (f)

Description of Anogmus? strobilorum. Thoms.

Female

Head broader than thorax, nearly 4 times as broad as thick in the middle, occiput concave; postocellar line more than twice occellocular line (12 : 5) which is itself $2\frac{1}{2}$ times the diameter of an ocellus. Viewed from in front the head is broader than high (33 : 25), narrowing below the eyes, truncate at the mouth, malar space .32 of the eye-height; antennal scrobe shallow; eyes large, ovate and bare; clypeus finely striated, rest of head finely reticulate: right mandible quadridentate, left mandible tridentate, maxillary palp. 4-jointed. Antennae 13-jointed, inserted below the middle of the head (23 : 17) in line with the lower extremities of the eyes, distinctly clavate, scape almost reaching the top of the compound eyes, subcylindrical; pedicel more than twice as long as broad at the apex, two-thirds as long as the ring joints plus the/

the first joint of the funicle; two distinct ring-joints, the first the smallest; funicle 6-jointed, the joints successively increasing in width; first funicle joint longer than the ring-joints combined; sixth funicle joint two times broader than long; club distinctly thicker than funicle, ovate, $1\frac{1}{2}$ times longer than the two preceding funicle joints, funicle and club clothed with pale hairs.

Thorax slightly more than $1\frac{1}{2}$ times as long as broad (35 : 22); pronotum short, dorsal aspect very transverse, slightly narrower than mesonotum, sculptured like the mesoscutum; mesoscutum very slightly convex, very finely reticulate at the sides, finely reticulate-punctate dorsally, about $1\frac{1}{2}$ times as long as broad (33 : 22), the parapsidal grooves present anteriorly but effaced posteriorly; scutellum reticulate-punctate but much more finely than the mesoscutum, about as long as broad at the widest point, convex, distinctly shorter than the mesoscutum; axillae finely reticulate; propodeum half as long as scutellum without a neck, a faint median carina at base of metathorax, no lateral folds; spiracular sulci absent; surface of propodeum reticulate-punctate, spiracles circular; pleurae finely reticulate.

Legs normal, coxae reticulate-punctate.

Fore wings nearly three times (98 : 35) as long as broad extending to the tip of the extruded ovipositor, bare basally; marginal cilia very short; marginal vein shorter than the post-marginal and more than $1\frac{1}{2}$ times as long as the stigmal vein (25 : 15). Abdomen conic-ovate, $1\frac{1}{2}$ times as long as thorax, shining, with [redacted] fine transverse ridges.

Ovipositor/

Ovipositor strongly exerted at tip visible portion more than $\frac{1}{4}$ of length of abdomen.

Head, thorax and abdomen a shining, metallic blue green, scape, pedicel and ring-joints of antennae pitchy-yellow, club of antenna black, mouth parts yellowish. Coxae concolorous with thorax, trochanters brown, rest of legs yellowish. Wings hyaline, venation testaceous. Compound eyes red.

Length 3.0 mm. (to tip of ovipositor).

Male

Sculpture of head, thorax similar throughout - finely reticulate punctate, abdomen shining and very finely reticulate.

Colouration is a shining, metallic blue green excepting the black-tipped pitchy-yellow antennae, red compound eyes, yellowish legs excepting the coxae which are concolorous with body.

The post-marginal vein of the wing is equal in length to the marginal vein which is itself $1\frac{1}{2}$ times as long as the stigmal vein (16 : 10).

Length 2.2 mm.

Section (g)

Trichomalus sp. near sunides Walk. - (determined by M. W. Graham of Oxford).

Female

Head broader than thorax, $3\frac{1}{2}$ times as broad as thick at the middle, occiput concave : postocellar line equal to 1.4 times ocellocular line which is itself 3.3 times the diameter of an ocellus. Viewed from in front the head is broader than high (37 : 25), narrowed below the eyes, truncate at the mouth; malar/

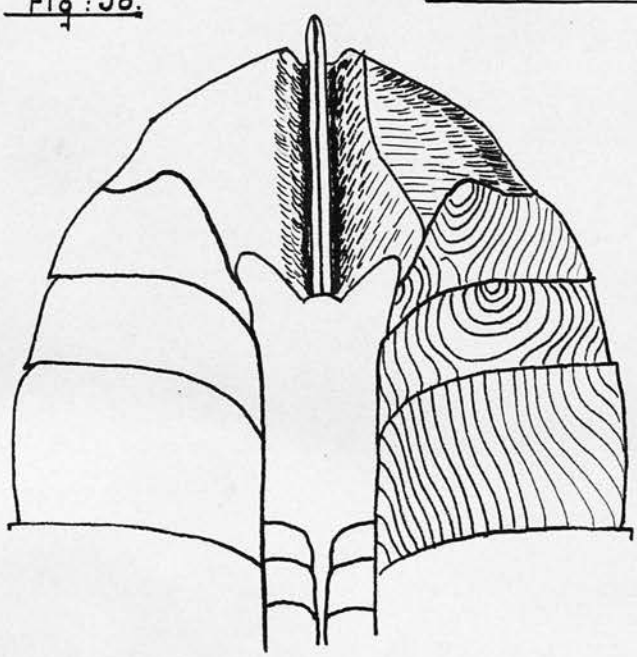
malar space equal to .4 of the eye-height; antennal scrobe extremely shallow; eyes large, ovate, bare; clypeus distinctly striated, rest of head nearly uniformly reticulate but on frons and cheeks reticulations merge imperceptibly into striations of clypeus; both mandibles with four teeth. Antennae 13-jointed inserted markedly below middle of head (28 : 16), distinctly clavate; scape not quite attaining the level of the compound eyes, subcylindrical; pedicel twice as long as broad at apex, not quite as long as the ring joints plus the first funicle joint, 2 distinct ring joints, the first smaller; funicle 6-jointed, first funicle joint a little longer than broad, about twice as long as the 2 ring-joints combined; club tends to be slightly narrower than 6th joint of funicle and as long as the combined length of the last 2 funicle joints. Whole antenna clothed with short hairs.

Thorax longer than wide (35 : 30); pronotum collar-like and conspicuously narrower than mesonotum; mesothorax coarsely reticulate punctate; mesoscutum as long as broad, parapsidal grooves very weakly impressed but discernable along entire length; scutellum slightly longer than broad (14 : 13), distinctly convex; propodeum (Fig. 52) as long as scutellum with a median carina, lateral folds very well developed and complete, spiracular sulci deeply impressed; surface of propodeum reticulate punctate but the well-marked "boss-like" neck region is extremely heavily punctate; spiracles circular; pleura sculptured like dorsum but more reticulate; sides of metathorax and propodeum densely covered with long hairs (these have been omitted from Fig. 52 to avoid obscuring surface sculpture).

Legs/

Fig : 56.

0·5 mm



Ovipositor (Ventral) of AMBLYMERUS APICALIS

Legs normal. Fore-wings 2.6 times as long as broad (83: 31) extending beyond apex of abdomen, bare basally; marginal cilia short; marginal vein a little longer than post-marginal (30 : 26) and $1\frac{1}{2}$ times as long as stigmal (30 : 20). Abdomen ovate as long as but broader than thorax, smooth and shining, apical segments dorsally and all segments ventrally show a fine reticulation. Tip of ovipositor just visible from above.

Whole body a shining metallic coppery green, antennal scape brownish, rest of antenna pitchy-brown. Coxae concolorous with thorax, rest of leg brownish. Wings hyaline. Compound eyes dull red.

Length 2.2 mm.

Section (h)

A Key to the Pteromalid Parasites of Megastigmus

Females

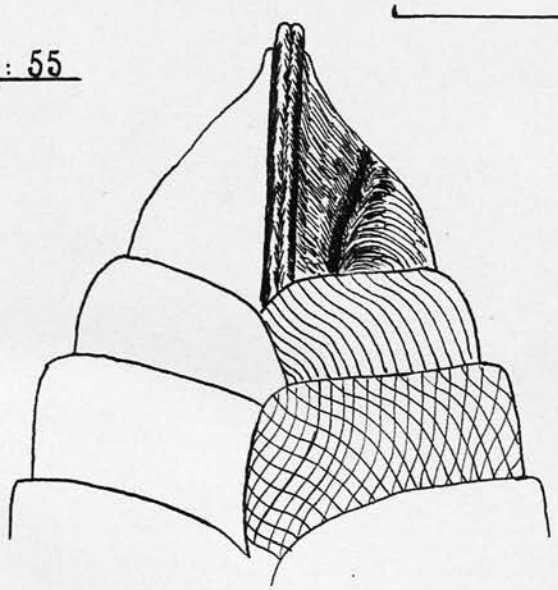
1(2) Ovipositor strongly exerted, reticulations of body surface very fine, whole insect blue-green in colour . . . . Anogmus strobilorum Th.

2(1) Ovipositor not strongly exerted. Insect coppery-green. Reticulations less fine.

3(4) Larger, usually more than 2.5 mm. long including ovipositor. Veins M and Cu. of fore-wing (Fig. 53) indicated by macrotrichia. Ventral abdominal sternites visible (Fig. 56). Propodeum lacking "boss" (Fig. 51). . . Amblymerus apicalis Th.

4(3)/

Fig: 55



Ovipositor (Ventral) of TRICHOMALUS NR: SUNIDES

4(3) Smaller, less than 2.5 mm. long including opipositor. Venation of fore-wing (Fig. 54) shows no M vein. Ventral abdominal sternites not visible (Fig. 55). Propodeum with a conspicuous bulbous enlargement posteriorly (Fig. 52) . . . . Trichomalus spp. near sunides. Walk.

Males

1(2) Abdomen with yellow-orange band. M and Cu, indicated on forewing by macrotrichia (Fig. 53) . . . . . Amblymerus apicalis Th.

2(1) No yellow-orange band on abdomen.

3(4) Body blue-green, propodeum without a "boss" . . . . Anogmus strobilorum Th.

4(3) Body iridescent coppery-green; propodeum with a "boss" (Fig. 52) M not indicated on fore wing by macrotrichia (Fig. 54). . . . . Trichomalus sp. near sunides. Walk.

Chapter V.

The Biology of Megastigmus spermotrophus

(a) Mating Behaviour

Records of copulation have been made by several workers. Noble described it for M. brevivalvus Gir (1938) and for M. acaciae in 1939 and Milliron (1949) gives a lengthy account of the procedure in M. nigrovariegatus. Ash.

In M. spermatrophus and M. pinus copulation was seen to occur within a few minutes of emergence from the seed and if a number of individuals of both sexes were confined in a vessel it was evident that "excitement" spread rapidly once copulation had begun by one pair. Within a few minutes all the males would be attempting copulation, even amongst themselves if there were fewer females than males. The male approaches the female and examines her with vibrating antennae, suddenly he will hold his antennae rigid at 45° whilst those of the female continue to vibrate. Keeping his feet stationery he oscillates the body from side to side until she approaches to within $\frac{1}{2}$ cm. when the male immediately takes up a mounted position on her back. The female finds the male but a slight encumbrance and can move easily, indeed a female M. pinus was observed to carry 3 males at once and still walk rapidly. The male stands on her back with front legs placed on her head, middle legs on the thorax and hind-legs on her folded wings. In initial courtship the antennae of the male vibrate very rapidly through a small arc, in close proximity to those of the female; occasionally he may raise his wings vertically, or, if the female is restive lower them over her body roof-wise. Throughout, the male vibrates his abdomen dorso-ventrally and periodically moves the antennae

through/

through a large arc to bring them into contact with the basal joints of the female antennae. Each of these larger sweeps is accompanied by a distinct lurch forward of the body during which the feet remain stationary, but the head is brought into contact with that of the female. (This procedure takes place about 50 times with 1 movement per second.) When ready to copulate, the female slowly elevates the abdomen and lowers the sterna in order to expose the genital opening. Instantly the male slips backwards and copulates caudo-laterally, whilst holding-on to the female's wings. Copulation lasts from 15-20 seconds. After copulation the male remounts the female and repeats his courting behaviour. One pair of M. spermotrophus were observed to complete 3 successive coitions within 10 minutes.

Milliron claims that in M. nigrovariegatus large males are not successful in mating with small females but he did demonstrate that forms of the species bred from different species of roses would mate if the sexes were comparable in size. During the studies under discussion here individuals of M. spermotrophus bred from seed in various parts of Great Britain were successfully mated with specimens reared from seed of American origin. But coition was never observed to take place between M. pinus and the extremely similar species M. milleri.

All the observations made and commented on so far took place in laboratories and so the paper by Balduf (1945) on field studies on M. nigrovariegatus is of interest. He observed that so long as a single female remained on a rose hip many males would remain in attendance in a state of some excitement. He suggested that the repeatedly observed segregation of males and females/

females indicated that any one female was inseminated only once in Nature. The males, remaining around old hips, tended to be in a different microhabitat from the females concentrating on the new hips for oviposition. In the absence of any noticeable behaviour on the part of the males seeking out females the only mixing of the sexes occurred at the emergence of both sexes from the old hips. In M. spermotrophus both sexes were found hovering around, or settling on, the current growth at the apices of the branches at all heights on the tree. Copulation was observed on these needles. Males were not seen to settle on the young cones, where, as the period of flight activity progressed the females were observed to rest for long periods. This behaviour may indicate that once inseminated the females move to this microhabitat unfrequented by males.

(b) Oviposition and Associated Behaviour.

The act of oviposition is easily observed in the field in many species and accounts of the process are given by Balduf (1945) and Milliron (1949) for M. nigrovariegatus and Miller (1916) for M. spermotrophus.

The female examines the whole surface of the cone (or rose hip according to species) with her antennae until a suitable site is located. The female then takes up a position on an ovuliferous scale, always facing the base of the cone in the case of D. Fir, normally inserting the ovipositor in the apical third of the exposed portion of the scale. When ready to oviposit the abdomen is elevated and the caudal end arched forward thus permitting the ovipositor to assume a perpendicular position at the mid-point between the widely spread middle and hind tarsi. The antennae, previously vibrating rapidly through

a small/

a small arc just above the cone surface, are now held motionless. Dorso-ventral body movements commence, accompanied by a bending of the legs especially the front pair, which produce a series of alternating thrusts and partial withdrawals so driving the ovipositor down. After some 30 - 60 seconds the ovipositor sheaths are released and resume their normal position whilst the ovipositor is forced down into the cone until the whole body rests close against the cone scale. The larger and rigid ovipositor sheaths assist in the initiation of drilling by preventing the ovipositor from bending laterally. After depositing the egg, the ovipositor is rapidly withdrawn, the whole operation having lasted from 2-5 minutes. Insertions of very short duration are presumably not successful in passing eggs. Milliron (1949) describes an interesting behaviour in M. nigrovariegatus in which a female after several successful egg depositions will take possession of a hip and excitably drive off other intruding females especially towards the end of the oviposition period. In M. spermotrophus such possessive behaviour has not been observed, indeed it is usual to find several females ovipositing in the same cone at one time. Between successive ovipositions the female frequently cleans its antennae with the "comb" device on the front tarsi. A series of egg depositions is frequently observed - one female was observed in the field to oviposit 5 times with 1 - 2 minute intervals in the same cone.

Miller (1916) by rapidly immersing ovipositing insects and cones in chloroform studied the path of the ovipositor within the cone. The ovipositor passed through the ovuliferous scale

on which/

on which the wasp was standing, and its underlying bract, until it reached the second or third scale below the cone surface. It passed down through the centre of this deepest scale almost to the base and then turned forward into the seed on its upper surface. Successful oviposition is restricted to cases in which the egg is deposited within the seed.

Miller found numerous cases in which the ovipositor did not penetrate as far as the base of the scale, especially where the cones had been become somewhat hardened. As the tissues become tough the ovipositor becomes bent and even stuck. Balduf (1945) records finding 5 females dead with their ovipositors in situ, whilst on June 11th 1951 at Bedgebury a number of cones were found with Megastigmus ovipositors in situ but with only a few abdominal sterna attached as if the wasps had been eaten by a predator whilst trapped by their ovipositors.

Milliron (1949) states that dissections show that M. nigrovariegatus does not contain eggs ready for deposition when newly emerged. Both M. spermotrophus and M. pinus were found to contain ripe eggs 4 days after emergence. M. nigrovariegatus and M. spermotrophus are both said to lay their eggs when the seeds are soft and the cotyledons enveloped in a watery or jelly-like medium. Miller found this condition when the cones were $1\frac{1}{2}$ inches long whilst in New Zealand Gourlay (1930) described such cones as small and green. In Germany Wolf and Zenck (1944) claim that cones are immune to attack by the end of June. Balduf (1945) reports that females of M. nigrovariegatus laid eggs over a period of 17 - 19 days in 1943 and 15 -20 days in 1944 although Milliron (1949) gives dates which indicate that

oviposition/

oviposition took place over a period of from 28-35 days in 3 successive years. At Bedgebury oviposition lasted about 3 weeks in each year of the study but as, at that station, two forms of Douglas Fir occur, the laying-period in the cones of each of the forms was more restricted.

The two forms of Douglas Fir which occur in Great Britain are the Oregon or Green type Pseudotsuga douglasii. Carriere and Blue or Colorado form P. glauca. Mayr. The latter is however very subject to severe damage by the leaf-cast disease Rhabdocline and so is rarely planted outside gardens and arboretums. The two forms are markedly similar excepting the cones which are quite distinct:-

P. douglasii.	P. glauca.
Young Cones green.	Young Cones pink.
Bracts only rarely reflexed.	Bracts always strongly reflexed.

The young pink female flowers are produced from 15th-21st April at Bedgebury by the opening of a "cone-bud" and within 4-5 weeks are suitable for oviposition. After 3 weeks the young cones are about 1 inch long and the pink bracts, almost $1\frac{1}{2}$ inches in length, become rather less "tight" and the pale pink (or green) cone scales become visible for the first time but the "cone" is still soft to the touch. In the case of P. glauca the exposed portions of these scales now become a deep reddy-pink in colour and the bracts reflex more acutely until they appear almost at right angles to the cone surface. At the time of oviposition these cones vary from $1\frac{1}{2}$ - $2\frac{1}{2}$ inches in length with the bracts exposed for $1\frac{1}{2}$ inches of their length. The cone scales are deep pinky-mauve except where they are overlapped by the scale below, where a narrow fringe of pale-green appears.

The bracts/

The bracts are pale-green with the mid-rib and lateral margins dark green. The cone is now hard and firm to the touch. P. douglasii on the other hand takes about 1-2 weeks longer to reach a suitable state for oviposition. At this time the cones are from $1\frac{1}{2}$ - $2\frac{1}{2}$ inches in length with the bracts up to $\frac{3}{4}$ inch in length and held quite tightly against the cone surface. The cone scales are a very pale green colour at first but later a reddy-brown colouration begins to appear at the bases of the scales and gradually affects all but their apical fringes. At the time this suffusion first appears the cones become suitable for oviposition but when it is complete the tissues have become so tough and hard that late-laying females become stuck fast by their ovipositors. Cones of P. douglasii become liable to oviposition by Megastigmus about June 4th - 5th in Kent and about a fortnight later in Evanton, Ross-shire.

From experiments in the laboratory where cones of all ages were offered to female Megastigmus it is apparent that the cones are only suitable for oviposition for about $2\frac{1}{2}$ - 3 weeks of their development. In a plantation therefore the phenology of the crop may extend this "danger' period considerably as at Bedgebury where P. douglasii and P. glauca occur together, so that there are cones suitable for oviposition for almost a month.

Lyons (1951) working on the insects affecting seed production in Red Pine found that he could in general divide a single cone into three regions, (1) a large, "unproductive" region in the lower half of the cone where the ovules do not develop (2) a large, central "productive" region where the ovules are developed at pollination and (3) a small, upper, "unproductive" region.

Similar/

Similar zones are discernable in cones of Pseudotsuga and the average percentage of the seeds in these regions are in Region (1) 25%, Region (2) 55.0%, Region (3) 20%. In all the hundreds of cones dissected eggs were only found to be laid in zone 2 except in years with a high density of Megastigmus females per cone.

During 1952 an attempt was made to ascertain whether the altitude of the cone above the ground had any effect upon the number of eggs laid therein by Megastigmus. A tree was selected which bore cones which had grown beyond the stage of successful oviposition and a number of cones were collected from various heights. The figures obtained show that whilst the percentage of good seed attacked did not vary discernably the intensity of attack as measured by the average number of eggs per seed did fall off with height. Such a result is not unexpected however, as the cones occur in the greatest numbers towards the tops of the trees so that the number of seeds available for oviposition becomes greater with increasing altitude.

Table 1.

Height of cones above ground	Number of seeds with					% Seed Infested	Av. Number Eggs per Seed.
	Nil	Eggs 1.	2.	3.	4.		
10 feet	97	108	30	6	6	60,7%	.85
25 feet	66	96	18	0	0	63.3%	.73
40 feet	36	48	0	0	0	57.1%	.57
80 feet	111	169	1	1		60.6%	.62

(c) The Flowering Biology of the Douglas Fir. Pseudotsuga.

Allen (1941, 1942 and 1943) has investigated the subject of seed-production in the Douglas Fir. The main results of his work/

Douglas Fir Seed - mature

Left - Good

Right - Shrunken

work are summarized here. The reproductive strobili are differentiated in August and may be recognized without dissection by the end of that month. Early in February the microspore mother-cell divides into 4 within the staminate strobili and by early March free microspores are produced which at the end of March become ripe pollen. The reduction division of the female megaspore mother-cell occurs early in March. Pollen remains in the micropyle of the seed for three weeks without germinating. The tip of the pollen-tube reaches the nucellus after a further 5 weeks penetrating the archegonium a week later. Thus, on an average, fertilization occurs 9 weeks after pollination.

With the cooperation of the students and staff of the Forestry Commission Forester Training Schools observations were made on the female flowers of Douglas Fir in 1952.

Site	Mean date Red Flowering Stage	Cones 2inches long.
Bedgebury, Kent.	April 21st	May 18th.
Lyndford, Norfolk.	April 28th	May 20th.
Forest of Dean, Gloucester.	April 24th	May 22nd.
Capel Curig, N. Wales.	April 20th	June 8th.
Glen Tress, Peebles.	April 27th	June 16th.
Benmore, Argyll.	April 10th	June 6th.

These figures indicate that throughout Britain the female flowers are pollinated in the last 2 or 3 weeks of April so that fertilization occurs during the last week of June and the first of July. Apparently pollination and fertilization have no effect upon the growth of the cone for it is normal for cones to produce seed without fertilization although such parthenogenetic seeds are usually empty. Empty seeds of this type, with shrunken and shr shrivelled white contents, are referred to in the general text as "shrunken."

Roeser (1942) following an 11-year study on trees growing in the Rocky Mountains showed that weather conditions at the time of flowering markedly influence cone-production. Under favourable conditions 90% of the "conelets" will be formed. But as they burst from the buds the flowers are most susceptible to freezing so that poor weather at "bud-burst" will adversely effect estimates of the cone-crop made the previous autumn. Allen (1941) showed that such estimates of the potential cone-crop could be based upon the ratio ovulate/vegetative buds.

If this exceeds .25 a very good crop should result whilst at from .15 to .20 a good crop should occur etc. According to Garman (1951) in good crop-years Douglas Fir trees on medium quality sites in British Columbia will carry an average minimum of 5000 cones per tree - as many as 20,000 per tree having been recorded. The viability of the seed produced in this natural habitat of the species ranging from 6 to 36% of the total seed produced. For purposes of natural regeneration a crop of 6000 cones per acre will restock the a rea with 3000 seedlings per acre.

Dispersal of the seed by natural shedding produces the density pattern of the Megastigmus larvae as they overwinter on the forest floor. In this connection the work of Siggins (1933) is of interest. He demonstrated that, when the wind direction was consistent, the seed fell in a V from the base of the tree. The length of the arcs of concentric radial zones increases as the square of the radii. Hence the greatest density of seeds would be at the base of the tree and a gradual decrease would occur to the point where the average seed was dropped by the average wind velocity. By experiments in a special shaft he calculated that the average rate of fall of a Douglas Fir seed was 4.4 feet per second. (Hence/

(Hence seed from a cone 40 feet up in a 10 m.p.h. wind would land 132 feet from the tree). Garman (1951) showed by his work on seed-dropping that Douglas Fir releases 78% of its seed by the end of October, retaining 20% for release in March. The poor quality cones shed their poor seed in September whilst the poor seed in the good cones falls in March. Thus the bulk of the good seed falls in September and October although the absence of low humidities may tend to result in a longer retention. In Garman's observations a downward trend in the relative humidity with a spell as low as 20% R.H. seemed to be the controlling factor - temperature appeared to have no effect.

In 1952 a number of seed traps were built and set out at Bedgebury, Kent to study the seed-fall from a 40' Douglas Fir there. The traps consisted of wooden boxes 3' x 3' x 3' and were placed around the tree North, South, East and West in 3 zones. 4 were placed around and adjacent to the tree stem, 4 at half the height of the tree away from the trunk and 4 more at a distnace equal to the tree height. The traps were examined and the seed removed fortnightly.

The results of this trapping, Table 2. suggest that 18.0% of the seed is shed in March but that under the local conditions seed fell regularly in the winter months with a peak in February due to abnormally high winds. The findings of Siggins (1933) that the greatest density of seed would be at the base of the tree is illustrated in Table 2.

From the figures in Table 2 it is possible to calculate the approximate density of the seeds falling per square foot of forest floor. At the foot of the tree 11 seeds fell fer square foot, at half the tree height away 5.0 and at a distance equal to the tree height 1.0.

Table 2.

Position of Traps		Month and Number of Seeds Trapped				
		Nov.	Dec.	Jan.	Feb.	March.
At base of tree	N.	2	18	24	31	23
	S.	6	23	26	51	24
	E.	3	14	19	26	17
	W.	6	10	18	36	12
	Totals.	17	65	87	144	76
At ½ TREE HEIGHT from bole.	N.	0	4	9	6	2
	S.	0	7	10	13	6
	E.	2	12	0	6	2
	W.	5	33	20	24	9
	Totals.	7	56	39	49	19
At TREE HEIGHT from bole.	N.	0	2	1	4	4
	S.	1	3	0	1	3
	E.	0	4	0	1	3
	W.	0	6	0	11	8
	Totals.	1	15	1	17	18
Monthly Totals.		25	136	127	210	113
Monthly Totals as % Total Trapped		4	22	21	35	18

The outstanding effect of the host tree on Megastigmus populations will be that of the size of the cone-crop in successive years. As is well-known the cone-crop of conifers varies irregularly from year to year. At present there is no single complete explanation of this variability nor any method of forecasting it. It is therefore valuable to enumerate those factors which are known to have an influence on seed production.

1. Age.

2. Vigour of Growth.

3. Environment - more seed on better soils etc.

4. Periodicity - (a) Spontaneous e.g bamboo every 33 years.

(b) Induced - requires an external stimulus.

It should be remembered that the female cones are initiated the previous August so that the condition of the tree at that time is important.

Kraus and Kraybill (1918) showed that excess Nitrogen promotes vegetative growth and that carbohydrates are stored by the tree, until external factors reduce the intake of solutes through the roots, so that the C/N ratio increases and reproduction occurs. Lochwing (1940) noticed changes in the nutrient distribution accompanying flowering and concluded that Nitrogen and Phophorus are the inorganic ions most closely associated with the transition from a vegetative to a flowering phase. He also emphasized the coincidence of drought with flowering. Drought retards the vegetative growth and increases the C/N ratio. Tiré (1935) commented on the fact that abundant flowering reduced the number of vegetative buds so that the reduced photosynthetic surface the following year reduced the possibility of two successive good cone-years. Garman (1951) reported 6 good cone-years within a period of 11 years in Douglas Fir in B.C. but it is generally assumed in Great Britain that a seed-year occurs in Douglas Fir every 5-6 years. However from the above account of the many factors attributing to such periodicity it is certain that foresters are a long way from an accurate method of forecasting seed abundance.

(d) <u>The influence/</u>

(d) The influence of cone development on Megastigmus.

The problem of studying the time of flowering of Pseudotsuga in relation to the weather conditions is obviously a long-term project beyond the scope of the present work. As is shown by the dates in the previous section considerable variations occur in the speed of development from the red-flowering stage to a cone 2 inches long. Cones of P. douglasii 2 inches long were taken as a point of reference for, in the previous section, cones of that length were found to be suitable for oviposition. In addition to geographical locations, the time of "ripening" for oviposition will vary in the same plantation, with elevation and exposure to sunlight within the canopy. Marked flowers at Glen Tress on "edge" trees were up to 10 days ahead of those on trees within the plantation. Genetic differences between trees also undoubtedly occur. The following dates of different phases of cone development in Douglas Fir were collected in the Forest of Dean during 1952.

Table 3.

	Tree 1.	Tree 2.	Tree 3.	Tree 4.	Tree 5.
Age in years	34	34	29	40	40
Ht. of cone in feet	52	54	35	45	50
Red-flowering stage	11th. April	11th. April	10th. May	14th. April	14th. April
Cone 1½" long	11th. May	11th May	15th. June	13th. May	13th. May
Cone 2" long	22nd. May	22nd, May	29th. June	22nd. May	22nd. May

Such variations, as in Tree 3, from the mean flowering date of the crop as a whole will provide some suitable hosts in early or late years (c.f. page 80).

The abundance of the cone-crop, dealt with in the previous section, and the periodicity of seed-years, referred to there,

will/

will obviously have a profound effect on Megastigmus populations. Seitner (1916) suggested that evidence obtained by him showed that the infestation of the seed tended to be heavier in poor seed-years. Regel (1951) agreed with this view and in addition claimed that seed-years following quickly one after another could effect an "extensive increase in the incidence of the insect". These theories are undoubtedly correct although it must be remembered that other factors can influence the proportion of seed attacked and so produce unexpected results. Such a case occurred at Evanton in 1952 when, although the cone-crop was only 1/5th of that of the previous year the % of good seed infested fell from 95% to 69%. Presumably the excessive density of female Megastigmus on the cones with consequent mutual interfence resulting in a reduction in the number of eggs laid by each female, was responsible.

The time of seed-fall will obviously determine the period for which the Megastigmus larvae are exposed to rodent attack. Collections of cones at various seasons of the year confirm Garman's (1951) observation that Douglas Fir retains up to 20%, mostly shrunken, of its seed until the March following ripening. At Evanton in 1952 collections of seed were made at the period of natural seed-fall. These showed that whereas the proportion of good seed present in the cones on the trees was only 21.0% the proportion falling naturally during mid-October was over 50%. This indicates that Garman was correct in attributing the main seed-fall of potentially good seed to October and November. Of the seed falling in autumn at Evanton 73% was infected with Megastigmus against 69.7% in the whole crop. This difference

is not/

is not significant but does prove that the bulk of the infected seed falls with the good seed to the forest floor in the autumn.

(e) Climatic tolerance of larvae.

No case of mortality was observed which could be directly attributed to excessive heat or cold but occasionally dead, dry or yellow larvae have been found in collections. Larvae will die in this manner if heated excessively and so a number of experiments were set up to determine the limits of heat resistance.

Chamberlin (1939) records that the mean difference between air temperature and the concurrent bark temperature of trees in full sunlight is 40°F. but the subcortical temperatures are high mainly because heat is able to travel inwards by conduction. In the case of a cone, the seed is separated from the ovuliferous cone-scale by a layer of air which increases in volume towards the periphery of the cone. In these circumstances more heat must be conveyed by convection so that one would not expect a 40°F. excess over air-temperature to be more than transitory. From temperature records at Bedgebury, Kent, it is obvious that the air temperature (shade) rarely exceeds 80°F, so that in Great Britain as a whole it can be fairly safely assumed that the temperature of the seeds would only rarely reach as high a value as 120°F.

Lots of 50 larvae were exposed to various high temperatures for periods of 1½ hours as follows:-

100°F.	50	Alive at end of exposure.				0	Dead at end of exposure.				
110°F.	48	"	"	"	"	"	2	"	"	"	"	"
120°F.	16	"	"	"	"	"	34	"	"	"	"	"

Exposures/

Exposures of lots of 50 larvae to a temperature of 120°F gave the following results:-

Period of exposure to 120°F.	N°. Alive	N°. Dead	% Mortality
1½ hours	50	0	0
1 "	35	15	30
1½ "	17	33	66
2 "	14	36	72
2½ "	0	50	100

In these circumstances it is considered unlikely that the seed-temperature would exceed 110°F long enough for mortality to result.

It was not possible to experiment with very low temperatures but as the larvae are in a state of diapause during the winter they will naturally have an increased resistance to unfavourable conditions. Many larvae were kept at 0°F for as long as 4 months without any mortality so that one can safely say that few larvae would die of cold under forest conditions in Britain.

Attention was also paid to extremes of humidity. Seeds were kept soaking in water for 4½ months during the winter and others at 100% R.H. Despite the fact that the seeds were covered with fungus adult Megastigmus emerged successfully.

If seed was kept at an R.H. of less than 20% for long periods the adults although fully formed seemed unable to cut an exit-hole in the dry, hard seed coat.

In the section on diapause in Megastigmus the water relations of the larvae are considered in some detail.

(f) Parthenogensis

Milliron (1949) was the first worker to show that a species of the/

of the genus i.e. nigrovariegatus was capable of facultative parthenogenesis. In 1951 a number of Douglas Fir cones were sleeved at Bedgebury during late April in order to make quite certain that no eggs would be laid in them by female M. spermotrophus. Virgin females, reared separately in tubes, were placed within these sleeves. The muslin was left in situ until June 1952 when they were checked for emergences. Of 10 cones, oviposition was successfully completed in 8 and from these 80 Megastigmus - all males - were obtained. Hence we may state that parthenogenesis does occur although only males are produced.

(g) Feeding-habits.

No records of the feeding-habits of the adults are given in the literature although Milliron mentions that he kept specimens alive on cotton-wool soaked in sugar-solution. In the experiments reported elsewhere in this paper split raisins were used successfully. At Bedgebury during the flight period much time was spent examining the flowers in the area to see whether nectar was being taken. No Megastigmus were, however, found away from Douglas Fir apart from a few hovering about the foliage of Tsuga. Two cases were observed where feeding took place in the field. In the first a female was seen to lick the globules of exudation on needles heavily infested with the sistentes of Adelges cooleyi. In the second, females licked the resinous surface of a young cone although this may also have been coated with some Adelges secretion, for a few sistentes were present amongst the scales. This observation is most interesting in view of the discovery by Eymin (1950) that contrary to widely held views the "honeydew" of Cinara pichtae is used by bees in Turkey as a source of protein.

It is/

It is conceivable that Megastigmus, like many other Chalcids, needs to assimilate protein before it can lay viable eggs and although phytophagous has developed this association with Adelges to make-up the deficiency.

The possibility that they may on occasion take nectar from flowers is not ruled out for Mr. C.N. Hawkins tells me that he swept a number of female Megastigmus from flowers at Minehead, Somerset on June 16th 1952.

(h) Field Activity of Adults.

A number of estimates of the period of seasonal activity appear in the literature but these will doubtless have been influenced by the latitude and altitude of the point of observation. Miller (1916) records that normally activity lasts for about 3 weeks in Oregon, covering the last week of April and the first 2 weeks in May. At 3000 feet activity is delayed until the end of May whilst at 4000 feet adults are not active until June. Most records refer to laboratory observations where the conditions of rearing are not specified but Escherich (1938) giving the period of activity as from March to August depending on the geographical situation and climate has undoubtedly placed the limits too widely. Hoffmeyer (1930) commented that he reared M. rafni, pinus and spermotrophus at room temperature in both summer and winter of 1st. year, the summer of the 2nd. year to which Wolf and Zenck (1941) have added spring of the 3rd. year. However the present study, as mentioned elsewhere, shows that emergence in the field is accomplished within a fortnight. That the initiation of activity is markedly influenced by climate was demonstrated at Bedgebury - for in 1951 laying commenced on

June 4th/

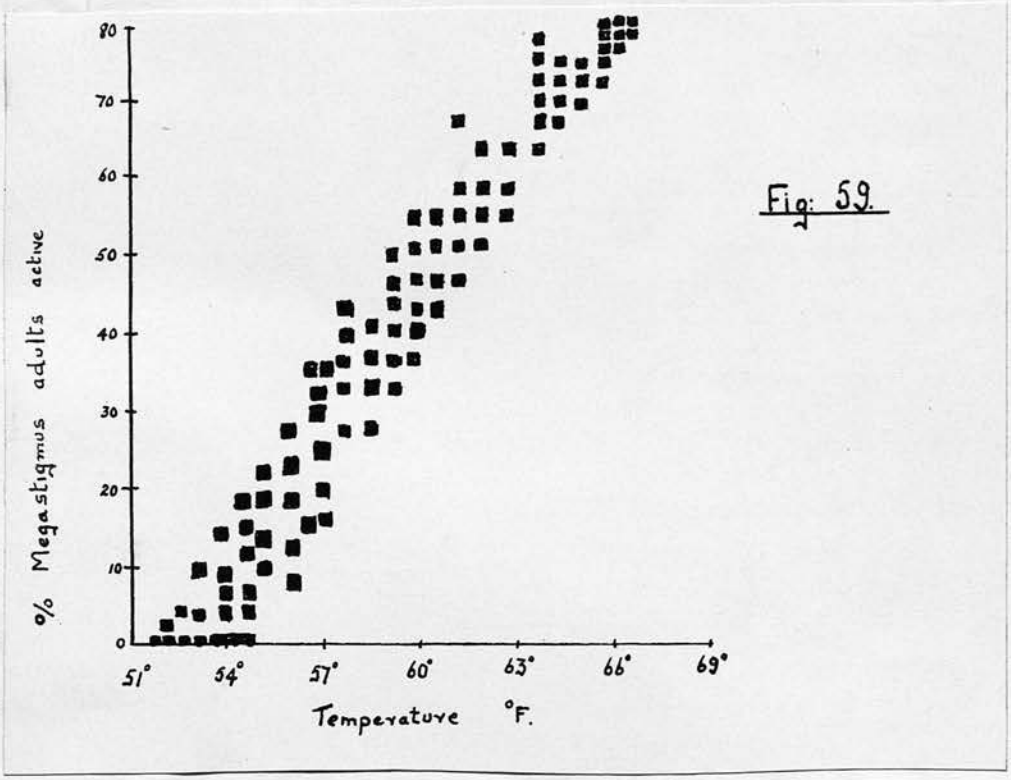

% Megastigmus adults active
80
70
60
50
40
30
20
10
0
51°
54°
57°
60°
63°
66°
69°
Temperature °F.

Fig: 59.

June 4th, a fortnight later than in 1952 and 1953. A comparison of the monthly mean temperatures in the pre-emergence months is as follows:-

	1951	1952	1953
March	40.6°F	43.8°F	44.2°F
April	42.5°F	48.2°F	46.7°F
May	50.5°F	54.7°F	52.5°F

During the four weeks of their activity the adults fly a good deal especially towards the apices of the branches where the buds are flushing or nearly flushed. Here they hover, especially on warm sunny days, settling on the needles frequently. Activity was observed in all weathers even with the wind at 20 m.p.h. but in such high winds activity was restricted to the leeward side of the trees. In very hot weather as Balduf (1945) found with M. nigrovariegatus, the adults tended to keep in the lower shaded portions of the crown. If disturbed from the foliage both sexes dropped downwards before resuming flight, a habit which facilitated capture with a glass tube. After the oviposition activity has proceeded for about a week the females tend to remain settled on the cones for considerable periods as many as 5 being observed on a single cone, without attempting oviposition.

By subjecting tubes containing adults to various temperatures a number of observations were made on the activity in relation to temperature. Thus any insect which was crawling, running or flying was assumed to be "active". When the % activity of the various samples was plotted against temperature a fairly well-marked band resulted, the mean threshold of which was 54°F and the minimum 51°F. (Fig. 59)

(i)/

(i) The Phenology of Megastigmus adult activity.

On Page 95 the threshold of development for the pupal phase of Megastigmus was calculated to be 42.5°F - using this value to compute the amount of heat in day-degrees to complete the pupal phase we obtain the following values from Table 7.

379.5, 376.0, 406.0, 390.0 = Mean of 388 day-degrees.

Utilising this information with relation to field observations and weather records at Bedgebury we obtain a very useful working index. The meteorological observations at Bedgebury are made in a Stevenson screen sited alongside the group of Douglas Firs studied there. By summing the daily mean temperatures above 42.5° from February 1st. onwards we find that:-

1951	1952	1953
Total of day degrees= 400° on June 4th.	Total of day-degrees= 395 on May 19th.	Total of day-degrees= 393 on May 22nd.
First female Megastigmus seen June 4th.	May 21st.	May 20th.

(j) Field Behaviour interpreted in the light of Olfactometer Experiments.

A number of experiments were conducted to demonstrate how great a part is played by the olfactory senses of Megastigmus in the location of its host and mate..

All the observations were performed in a window-less incubator maintained at 77°F. The type of olfactometer used was that suggested by Grosch (1950) who had worked on male Braconids. The apparatus consisted of a simple T-shaped tube placed in a vertical position. The insects under test were

placed/

placed at the lower end of the vertical arm in a 3" x 1" vial. Responding to negative geotropism the insects crawl up the vertical tube for 4 inches to the point of choice from which horizontal arms (each 2 inches in length) lead to trap vials. These trap vials, also 3" x 1" tubes, were fitted with corks through which the horizontal arm protruded with a tapering aperture to reduce the possibility of escape. Each test lasted two hours when the apparatus was removed from the incubator. After a test the apparatus was washed out, dried and aired before re-use. Provided sufficient numbers were employed their distribution should indicate an attraction to or repulsion from the test material.

Males of M. spermotrophus were tested first in the apparatus with females as a lure in one trap and nothing in the other. The second series compared the attraction of Douglas Fir foliage for males, the third for females. In the fourth and fifth series of experiments adult male and female M. pinus were tested with foliage of Abies grandis and Abies nobilis. Series six and seven compared the reactions of fertilized and unfertilized to host foliage.

Results and Conclusions

Material Tested	No. with test material.	No. in zero traps.
I Female M. spermotrophus(5)	18 males 14 17 13	12 16 13 17
II Douglas Fir foliage	27 males 28	23 22
III Douglas Fir foliage	19 females 22	31 28
IV Abies grandis foliage	21 M. pinus reared 20 on nobilis	29 30

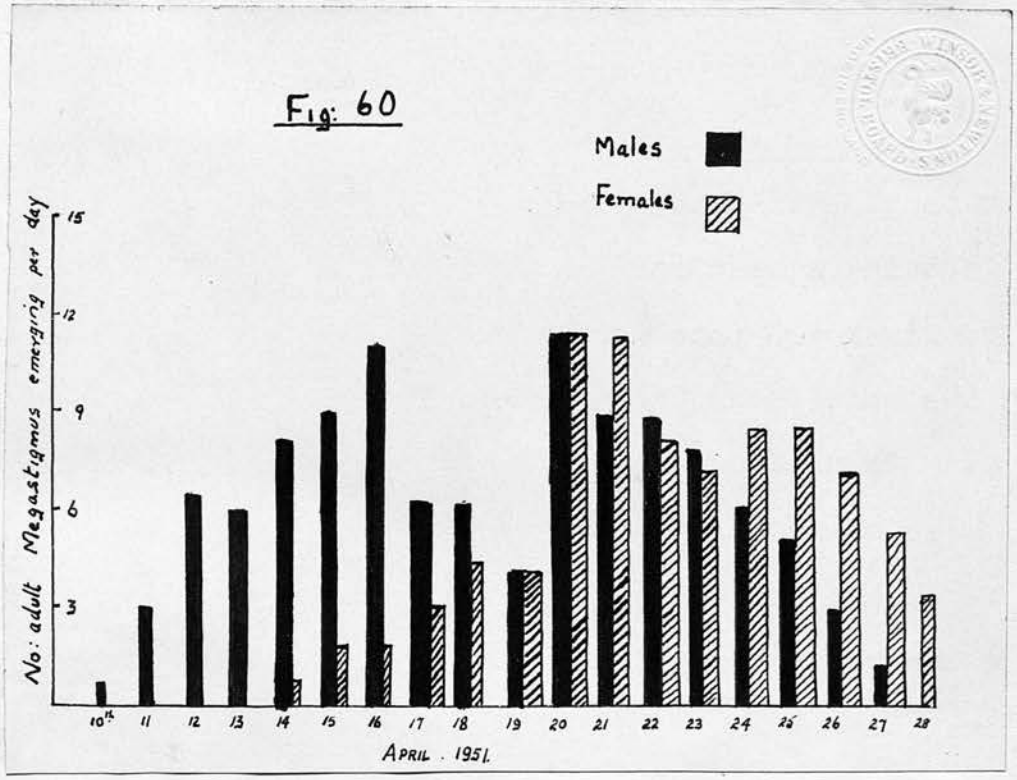
V/

Material Tested	Nº. with Test Material	Nº. in zero trap.
V Abies nobilis foliage	32 M. pinus reared	18
	25 on nobilis	25
VI Abies nobilis foliage	14 Unfertilized	11
	12 female M. pinus	13
	13	12
	10	15
VII Abies nobilis foliage	18 Fertilized	7
	16 female M. pinus	9
	17	8
	18	7

From this series of tests we may draw the following conclusions. In a closed system of the type used males do not receive a directional stimulus from the females unless the latter are within a few millimetres of them. The males under test did, as with Grosch's Braconids, exhibit evident signs of stimulation, waving their antennae as in pre-copulatory behaviour, but this perception of the female seemed only to lead to an extension of random search. Once in the vial with the females copulation ensued when the sexes approached within a centimetre or so of each other. In nature this apparent necessity for close proximity of the sexes before they are stimulated to coition is assured by both sexes being attracted to the same microhabitat, the ends of the shoots of the host trees. If captive adults were released on the forest floor they at once flew almost vertically upwards and then hovered around, and occasionally landed on, the apical shoots of one of the lateral branches. The lack of directional stimulus from conifer foliage is shown by the random distribution in Series II to V above and no doubt accounts for the fact that in mixed plantations Megastigmus can be found hovering around the branches of many

species/

Fig: 60


Males
Females
No: adult Megastigmus emerging per day
15
12
9
6
3
10th
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
April . 1951

species of conifer as in the mixed collection of conifers in the Arboretum at Bedgebury.

Series VI and VII suggest that following fertilization a female Megastigmus becomes more susceptible to the stimuli emitted by their host and hence reduce the area of their random search for cones.

(k) Emergence of adults.

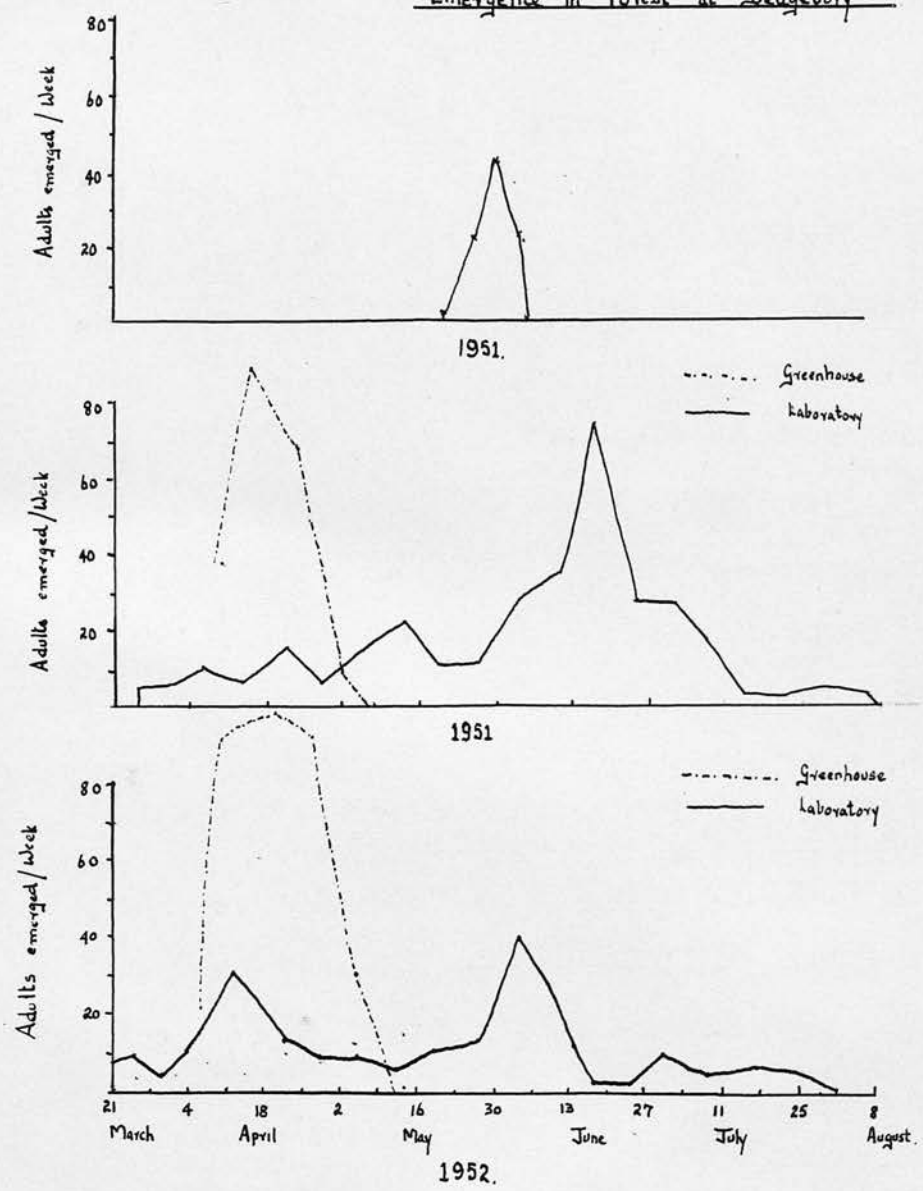
Adults of both sexes bite their way out of the seed by cutting a neat round hole in the testa; emerging head first and once the legs have obtained a purchase on the outside of the seed coat, pulling themselves out. As mentioned later in this section the variation in size of the adult Megastigmus precludes using the size of the exit-hole as a clue to parasitization, for the range in size of the host overlaps that of the parasite.

Milliron (1949) observed that the males of M.nigrovariegatus emerged about 3 days before the females and experience with both M.spermotrophus and M.pinus indicates that the same occurs in these species. In each year the first male was seen from 2-4 days before the first female. The pattern of emergence in M.spermotrophus from a sample of Douglas Fir Seed is depicted in Fig. 60.

Hoffmeyer (1930) and Wolf and Z enck (1941) both claim that indoors the adults of the seed-infesting forms emerge over a period of three years with various peaks of emergence during the spring and summer of each year. A similar extended period of emergence

Fig: 58.

Emergence in Forest at Bedgebury



was observed in the course of the present study, but taking any one year it was shown that exposure to normal outside, or greenhouse, conditions produced a much shortened emergence period compared with that in the laboratory (Fig. 58). Apparently laboratory conditions with the mean temperature at about 60°F throughout the year affect a break in the diapause of some individuals very slowly whereas the cold winter, and higher spring, temperature of the field and greenhouse, cause an earlier but at the same time more sudden break in diapause.

A most noticeable feature of Megastigmus populations is the range of size of the individuals which was shown to be correlated with seed-size. Two lots of Douglas Fir seed, one conspicuously larger than the other, were selected and the resultant adults measured:-

Seed Lot A.	Seed Lot B.
Length 5.75 ± .23mm.	Length 7.2 ± .24mm.
Breadth 1.8 ± .11mm.	Breadth 2.1 ± .09mm.
Wt. of 20 seeds .08gms.	Wt. of 20 seeds .12gms.

The calculated value of "t" for the difference between these two samples was 2.12 showing that Sample B was indeed significantly larger than Sample A.

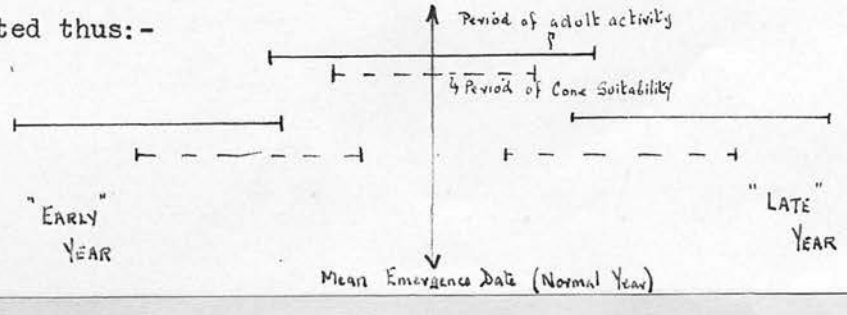
The size of the adults was estimated by measuring the length of the forewings of the females:-

Ex. Sample B.
1.46, 1.50, 1.50, 1.53, 1.48, 1.52, 1.52, 1.50 mm. Av. 1.50mm. ± .009
Ex. Sample A.
1.34, 1.25, 1.34, 1.28, 1.28, 1.30, 1.32, 1.33 mm. Av. 1.31mm. ± .013.

The "t" test applied to these results again gives a value of 2.12 so that it is possible to say that the significantly larger seed produced significantly larger adult Megastigmus.

From the standpoint of bionomics the crucial point will be whether circumstances can arise in which a portion of the seed escapes oviposition because the cones are late or early in relation to Megastigmus emergence. In this connection the claim by Wolf and Zenck (1941) that cold weather delays the development of Megastigmus more than that of the flowers is of interest. The present study indicates that normally adult female Megastigmus are on the wing over a longer period than that during which the cones are suitable for oviposition. Hence in a "late" year a proportion of the cones will have developed too far for successful oviposition by the late emerging chalcids. In an "early" year the chalcid population will decline and die out before some cones have reached a suitable stage for egg-laying, as happened in 1952. In that year the wasps had been on the wing for 3 weeks before the cones of some P. douglasii had become suitable for oviposition and although late counts showed that all the females were concentrated on these cones a high proportion of the seed escaped attack. The average number of eggs per seed being only 0.17 whilst in the earlier cones of P. glauca a level nearer 2.0 eggs per seed occurred. In 1953 a year with a very similar Spring climate to that of 1952 the values were 0.14 eggs per seed in P. douglasii and 1.9 in P. glauca.

The interrelationship of these events in phenology can be depicted thus:-



(1) Sex Ratio

There are a number of references in the literature to this matter which taken together provide a confusing pattern. Mc Dougall quotes Crozier as breeding 142 male and 40 female M. spermotrophus whilst he obtained 19 males and 30 females himself. Hoffmeyer (1930) reared 43 females and 31 males and Escherich (1939) comments that 211 females and 161 males of M. strobilobius were reared but no males of M. suspectus were obtained. Wolf and Zenck (1941) reported that in the first year's rearing, females outnumbered males by 5 : 1 but that the following year only males were obtained. The most extensive observations for any species of Megastigmus are provided for M. nigrovariegatus by Milliron (1949) and Balduf (1945). The former estimates the ratio of female : male as 1.0 : 1.15 the latter as 1.0 : 0.91.

Naturally one would expect the ratio to vary from species to species and year to year, but following collections of infested seed from all over Great Britain it was obvious that marked differences also occurred in the same year between different localities. For example in 1951 males of M. spermotrophus outnumbered females in 27 localities, whilst the reverse relationship existed in 26 other forests. Sometimes as at Bedgebury the preponderance of females was most marked, the sex ratio being as low as .25. However, pooling all available records for 1951 and 1952, 2775 males and 2841 females were reared which suggests a mean sex ratio of .98. The average ratio of females : males in M. pinus where 765 males and 938 females were reared was .81. In M. seitneri there appears to be only a few males,

for out/

for out of 108 reared only one was a male - hitherto undescribed.

A paper by Flanders (1939) provides a most interesting commentary upon that wide range in sex ratio referred to above. He found that in arrhenotokous species of Hymenoptera the sex is determined during oviposition. Since the spermatheca of the female contains only female-producing sperms and is stimulated by the passage of eggs down the vagina it follows that mated females would produce only female offspring unless the spermatheca is under some external regulation. He concluded that the reflex controlling the discharge of sperms involves the spermathecal gland, the fluids in which are apparently alkaline. At fertilisation the sperms are deposited in the vagina and a CO_2 gradient is established which governs their locomotion to the spermatheca when they become inactivated by the concentration of their own CO_2. When a mated female oviposits in a preferred host the sperms are reactivated by secretions of the spermathecal gland which reverse the CO_2 gradient so that when the sperm valve is opened the sperms swim down the duct to the egg. If the discharge of sperms is inhibited by a high oviposition rate under conditions of high host density than an internally influenced sex ratio results. The spermatheca is more frequently inactive when oviposition occurs in an unpreferred host or at a high rate of oviposition and hence males are produced.

It is therefore probable that the differences frequently occurring in sex ratio are due to external local factors. It is interesting to record in this connection, that at Rosehaugh in 1951 and 1952, when the density of Megastigmus per acre was very high (16 adults per cone) the resultant adults were preponderantly males. This/

This result was presumably due to the number of eggs which had to be laid in unpreferred hosts. At all the lower densities observed in this study females outnumbered males.

(k) Longevity of adults.

Milliron's study on M. nigrovariegatus, in which he distinguished between laboratory data and field observations, provides the only really detailed work done previously on longevity. To study the latter he confined adults within muslin-covered quart jars in the open, feeding them with brown-sugar solution on a cotton plug. In these conditions the average life of males was 8.45 days and females 11.04 days. Under laboratory conditions with temperature and humidity controlled both males and females lived 9 days but if the temperature was raised to 30°C the longevity fell in both sexes to 5.8 days whilst if the temperature was lowered to 15°C the males lived to 36 days and the females 49 days. The maximum longevity recorded at this temperature was 73 days in a male and 87 days in a female. These figures approach the records of Seitner (1916) who recorded a female M. strobilobius living 59 days and a female M. suspectus 52 days.

At 15°C M. spermotrophus kept in tubes and fed on split raisons the average longevity of 121 males was 6.9 days and of 125 females 9.5 days. Adults of M. milleri lived exactly the same period but in M. pinus

the males/

the males only lived 4.4 days and females 6.4 days.

If the temperature was raised to 33°C (91°F) the longevity of males and females became less than a day but at 7°C (43°F) the males lived 14.9 days, females 19.4 days; and at 4°C (39°F) males lived 16.9 days and females 21.0 days.

Wolf and Jenss (1941) postulated that in the forest females would normally live for about a month but Milliron suggested that the maintenance of the normal population of M. nigrovariegatus through the season of activity was due to the daily emergence of adults over about a month - once the rate of emergence decreased the general population level began to fall. Such a situation apparently exists in M. spermotrophus although the emergence period is more restricted, about 14 days, so that the longevity of the late emerging females determines the length of the oviposition period. The duration of this activity indicates that the longevity of the females in the field is about 20 days.

The Problem of Diapause.

Literature concerning the phenomenon of diapause has reached considerable proportions but the recent paper by Andrewartha (1952) has ably brought together the main theories and conclusions of workers in this field.

It is clear from the work of Wigglesworth (1950) that ecdysis during the larval and nymphal stages is under hormonal control. When diapause occurs in a

nymph/

nymph, larva or pupa the particular hormone lacking so preventing continued growth, is one produced by the neuro-secretory cells of the brain. The hormone theory is concerned, however, only with the final stages of diapause and offers no explanation of how these neuro-secretory cells come to remain dormant or what ultimately induces the diapausing individual to secrete the hormone again. Andrewartha states that it is reasonable to conclude that the basic difference between a diapausing and a non-diapausing individual resides not in some intrinsic quality of the endocrine organs themselves but in some tissue external to them which in appropriate circumstances may stimulate the neuro-secretory cells to produce their secretion. Bounhoil (1938) established that the neuro-secretory cells are not stimulated unless a minimum amount of food is ingested. This food is built into reserves in the fat-body and concurrently broken down so that the endocrine cells may be stimulated after these breaking-down processes have reached a threshold value. Diapause may thus be the outcome of an unbalance in metabolism where building-up processes go on normally but the breaking-down processes are reduced to a minimum. There is in the literature on the ecology of diapause much evidence to suggest that the universal "cause" of diapause is the accumulation of food reserves which have not yet been broken down in preparation for the next stage in morphogenesis. However Steinberg (1936) working with Loxostege sticticalis. L. showed that the larva required 85% water and 15% solids to build up

protoplasm/

protoplasm and that if insufficient water was absorbed the fluids present in the body were bound by the protoplasm and the insect went into diapause.

Megastigmus is univoltine and all individuals of each generation undergo diapause. An interesting point bearing on the bionomics is the varying duration of diapause amongst individuals of the same generation.

The resumption of development of insects in diapause is promoted by a number of factors, one of the commonest being the need for rest at low temperatures. This temperature may have to be near the freezing-point or merely below the threshold of development. While diapause is usually overcome most satisfactorily after exposure to low temperatures it may, in some instances, be overcome gradually at developmental temperature. The response to temperatures favouring development is often more marked in proportion to the duration of previous exposure to low temperature.

Townsend (1926), having cited numerous instances in which the beginning of hibernation was marked by a reduction of the water content of the organism, postulated that the most important factor breaking the diapause of the Codling Moth is the readsorption of water by the tissues which speeds up enzyme activity. Babcock (1924) working on the European Corn Borer showed that to promote a break in the diapause the first six weeks of cold-rest must be at a temperature below the threshold of development but later the limiting factors were warmth and water. He also demonstrated, as did Rice (1937) with Epiblema strenuana, that contact water must be supplied - high humidity was not sufficient. Very extensive studies were undertaken by Prebble (1941) on the diapause

problem/

problem in the sawfly Gilpinia polytoma. Hartig. (=hercyniae) in which development may be suspended for varying periods of up to 7 years. He demonstrated a progressive response to favourable developmental conditions as the period of cold-rest was extended for 2 or 3 months - the degree of cold was unimportant as long as it was below the threshold of development. An incubation temperature of 75°F caused a higher percentage of individuals to break diapause than one of 65°F, but there was little difference in the percentage of development within the limits 45°-65°F. The percentage of development after appropriate cold-rest and at an incubator temperature of 75°F was in all cases much lower in unsaturated atmospheres than in saturated.

Agrell (1951) contributed a number of suggestions to the diapause problem as the result of his work on Phalera bucephala L. (Lep). He produced evidence of a change in the thermal coefficient of respiration with lowered temperatures, which indicated an additional effect of a secondary component in the respiratory metabolism which had a lower thermal coefficient than ordinary respiration. This caused the metabolism to be relatively high in cold conditions and suggested that diapause can be broken by exposure to low temperatures because the development rate though low in diapause increases to a maximum with decreasing temperature. He calculated the respiratory qutient during diapause as 0.35 which indicated an incomplete combustion of fat into carbohydrate. He showed that the R.Q. increased with developmental age but that at low temperatures (+5°C) with an R.Q. of 1.0 only complete combustion is possible. With rise in temperature the R.Q. decreases so that he postulated two antagonistic processes. The hormones controlling

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development/

development can only be formed at low temperatures by the process of complete combustion but on the other hand this process is progressively less dependent on temperature for its existence as the R.Q. rises with developmental age. He therefore concluded that the hormone catalysed the same or a similar process which was the cause of its own origin. An unstable catalyst was kept in existence by the occurrence of reactions which it catalysed.

(m) Diapause in Megastigmus

Megastigmus larvae undergo a true diapause, as distinct from quiescene, for returning 'resting' larvae to high temperatures without a period of cold-rest will not induce pupation. Bearing in mind the changes which occur in the larval diet - from the watery contents of the young seed to a drier endosperm in July - it is probable that the changing composition of the food is the chief 'cause' of diapause in Megastigmus. Squire (1940) found with Platyhedra gossypiella that the variations in the relative proportions of fat and water were the most important of these changes. Presumably the complete exhaustion of the food available within the seed will "fix" the tendency to diapause initiated by the gradual drying-out of the endosperm.

Escherich (1938) commenting upon diapause in Megastigmus spp. queried whether one or all of the following factors contributed to it (a) Endogenous factors (b) Adaptation to irregular fructification periods of host and (c) Climatic conditions especially temperature and availability of water. Seitner (1916) recorded that larvae of M. strobilobius were unable to develop in the spring if conditions were too dry, which suggests that addition of water would have induced the larvae

to break/

to break diapause.

In an attempt to investigate some of these factors a number of experiments were conducted with larvae of M. pinus. This species was chosen as seed from an exceptionally heavy infestation was available and the large larvae are more easily extracted without damage from their host seed than any other species.

The experiments which were made can be conveniently discussed under two headings:

1. The effect of temperature.
2. The effect of humidity and contact water.

(1) Effect of temperature.

In all observations on the effect of temperature on the breaking of diapause lots of 50 or 100 seeds were used. In October when the seed was received from the forest it was placed in a refrigerator at 38°F. Each week samples were removed from this low temperature and placed in constant temperature cabinets. All emergences from the seeds were observed and the date recorded so that the mean date of emergence of the adults in each sample was determined. When emergence for the year was complete the seeds were dissected and the number of larvae overwintering for a second year counted. Table 4.

The effect of submitting larvae to 10 weeks of cold-rest following progressively longer periods at laboratory temperatures was tested with the results shown in Table 5. These show that despite a difference of as long as two months in exposure to the laboratory temperature of 58°F the developmental period remained approximately the same although the proportion of larvae continuing in diapause tended to decrease. Hence we may infer

that/

Table 4.

	Number of weeks cold-rest		0	1	2	3	4	5	6	7	8	9	12	15	20	23	25	27	30	40
Temp. 77°F.	Number of larvae exposed	1951	38	41	43	35	40	38	39	54	50	42	106	38	98	100	-	100	-	-
		1952	100	100	100	100	100	100	100	100	100	100	100	100	100	100	100	98	97	100
	Number of adults emerged	1951	Nil	Nil	Nil	Nil	Nil	5	6	24	26	24	56	25	68	68	-	50	-	-
		1952	0	0	0	0	0	12	14	40	50	55	54	70	72	68	66	53	42	25
	Mean duration of exposure to 77°F before emergence	1951						40 days	34 days	31 days	30 days	29 days	26 days	21 days	12.8 days	11.0 days	- days	38.0 days	- days	- days
		1952						40 days	33 days	30.6 days	29.6 days	27.8 days	26.2 days	20 days	13.0 days	11.0 days	15.2 days	39.2 days	62.4 days	106 days
	Percentage larvae in 2nd. diapause.	1951	100	100	100	100	100	86.8	84.6	55.6	48.0	42.9	47.2	34.2	30.6	32.0	-	50.0	-	-
		1952	100	100	100	100	100	88	86	60	50	45	46	30	28	32	34.0	48.0	59.8	75
Temp 66°F.	Number of larvae exposed	1951	37	45	41	38	38	35	44	38	35	41	100	40	101	100	-			
		1952	100	100	100	100	100	100	100	100	100	100	100	100	100	100				
	Number of adults emerged	1951	Nil	Nil	Nil	Nil	Nil	Nil	7	16	15	18	47	24	62	59				
		1952	0	0	0	0	0	0	15	40	41	41	48	62	65	58				
	Mean duration of exposure to 66°F. before emergence	1951							42 days	40 days	38 days	36 days	35.3 days	29 days	19.2 days	36 days				
		1952							43 days	40 days	37.2 days	35.4 days	34.7 days	29 days	19.5 days	36 days				
	Percentage larvae in 2nd. diapause.	1951	100	100	100	100	100	100	85	60	59	59	52	38	35	42				
		1952	100	100	100	100	100	100	84.1	58.0	57.1	56.1	53	40	38.6	41				

Table 4. (cont.)

Temp.	Number of weeks cold-rest		12	15	20	23	Temp.	12	20
58°F.	Number of larvae exposed	1951	100	-	100	100	47°F.	100	100
		1952	100	100	100	100		-	-
	Number of adults emerged	1951	45	-	61	53		44	52
		1952	40	48	65	51		45	50
	Mean duration of exposure to 58°F before emergence	1951	58 days	50.2 days	39.6 days	55.7 days		152 days	97 days
		1952	60 days	- days	37.2 days	56 days			
	Percentage larvae in 2nd. diapause	1951	55	-	39	47		56	48
		1952	60	52	35	49		52	50

Table 5.

10 weeks of exposure to cold-rest.	Duration of exposure at 77°F. after 10 weeks Cold-rest before emergence	% Larvae continuing in Diapause
27th October - 8th January	28.0 days	45.0
10th November-22nd January	29.6 days	48.2
25th November- 6th February	29.3 days	40.2
8th December-19th February	28.0 days	32.0
20th December- 3rd March	29.2 days	31.6

that development before cold-rest in the autumn was almost nil. Reference to Table 4. shows that even with exposure to 77°F a minimum of 4 weeks cold-rest was necessary before development could proceed. Larvae denied this cold-rest were kept at 77°F for as long as 2 years without further development although they remained alive. At 66°F 5 weeks exposure to cold was necessary. At laboratory temperatures without cold-rest development did take place the following spring and summer, but as demonstrated earlier with M. spermotrophus, the period during which adults emerged extended over several months instead of 7 or 8 days as in samples subjected to low temperatures. Of laboratory material (kept at about 58°F)dissected following emergence only 6% were found to be in prolonged diapause whilst all the values quoted in Tables 4 and 5 are above this. The tables suggest however that the proportion in 2nd diapause decreases the longer the removal from cold-rest to higher temperatures is delayed. At 77°F following 6 months cold-rest (up to the end of March) it is evident that (1) the proportion of 2nd diapause larvae increased again and (2) the duration of exposure to the higher temperature began to increase. This lengthening of the developmental period could indicate a cyclical phenomenon in the diapausing larvae

Which/

which is brought about by the response to higher temperatures rising gradually to a peak and then falling off. The observed effect of an increase in the duration of exposure of the seed to higher temperatures before emergence could be due (a) to increase in period of time before initiation of prepupal phase or (b) to a lengthening of the pupal period.

To elucidate this problem a number of larvae were extracted from the seed, following various periods of cold-rest, and placed in small Petri dishes. The naked larvae were examined every day and the date of the defaecation - which indicates the start of the prepupal phase - noted.

Table 6.

Temperature.	77°				66°			58°	
Period of Cold-rest in weeks.	9	12	23	30	9	12	23	12	23
Mean duration of pupal phase.	11	11	11	11	16	16.2	16	26.8	27.2
Number of days before defaecation.	18	15	0	51	20	19	20	34	29

These results show conclusively that once initiated the length of the pupal phase is determined by the environmental temperature. The observed lengthening of the period of exposure to high temperatures, following cold-rest, takes place before the pupal phase is initiated. Following the reasoning of Agrell it would seem likely that the R.Q. increases with developmental age only up to a certain maximum and then decreases.

From the standpoint of field populations however it is evident that the small variations in the amount of heat experienced by larvae in any spring will fall between too narrow limits to influence to any extent the proportion which enter prolonged diapause. There will prboably be a tendency for prolonged

diapause/

diapause to be at a minimum following very severe winters for the experiments show that at all temperatures tested the percentage of larvae in extended diapause decreased with increased exposure to cold. As Prebble found with Gilpinia the degree of cold experienced did not influence the results as long as it was below the threshold of development. A few seeds were kept at 32°F for 12 weeks but the emergence results coincided with those in the tables. It should also be noted that comparing samples of larvae which had received the same period of cold-rest, more larvae developed at 77°F than 58°F. This result suggests that an abnormally warm spring would also tend to increase the proportion of larvae becoming adult.

From the data recorded in this section it is instructive to calculate the threshold of development. This may be done using the method of Sanderson and Peairs (1913) by plotting the reciprocal of the duration of development against the appropriate temperature

Table 7.

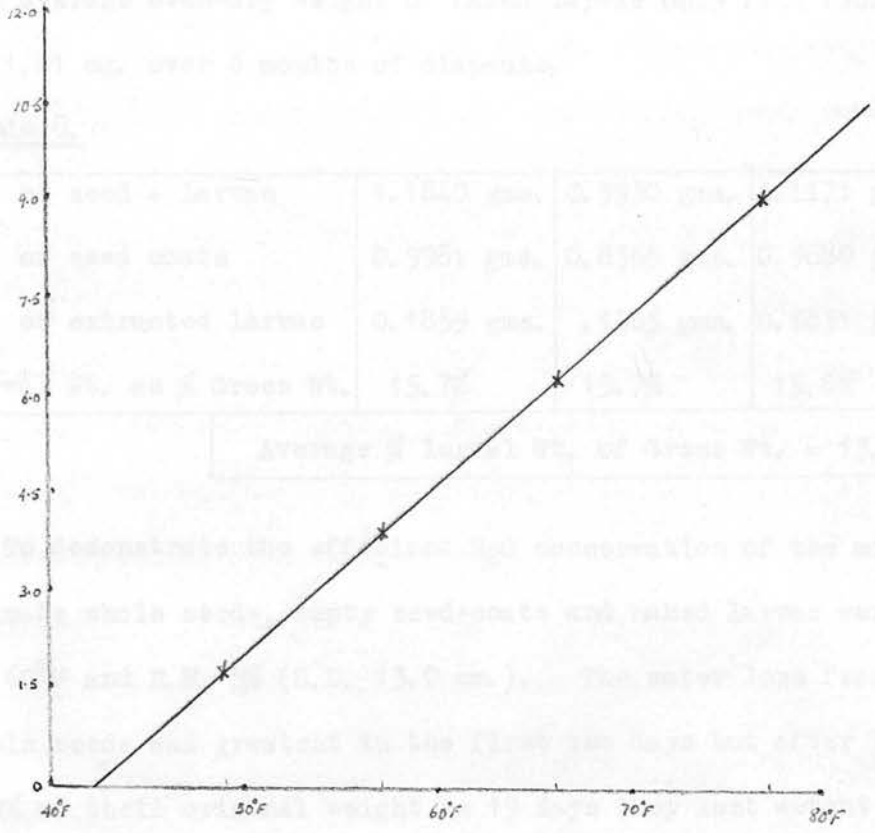
Length of Pupal Phase	11	16	28	60
Reciprocal	9.1	6.3	3.6	1.7
Temperature	77°	66°	57°	49°

The graph, Fig. 61, indicates a threshold of development at about 42.5°F. It is well-known that such a simple linear relationship between temperature and development does not hold in the lower temperature range so that the actual threshold of development is probably somewhat below 42.5°F. As the females, requiring slightly more heat, emerge later than the males the fact that Fig. 61 has been constructed from the mean emergence

periods/

periods of both sexes provides a useful practical reference if $42.5^{\circ}_{F.}$ is taken as the developmental zero of the females.

Fig. 61.



(2) The Effect of Humidity and Contact Water.

Ullyett (1938) studied the function of the cocoon in maintaining the micro-climate of Microplectron fuscipennis and Prebble (1941) adopted his methods in experiments on the role of the cocoon in regulating the water exchanges of Gilpinia. The reasoning employed by these investigators has been used as a basis of the following conclusions.

The larvae of M. pinus were found to make up 15.8% of the gross weight of the seed of Abies nobilis in the autumn. Their water-content, calculated by heating to dry-weight in an oven at 100°C for 3 hours, was found to be 57.7% of their live-weight

which/

which in November was 4.63 mg. The subsequent values assume that all the weight loss occurring was due to water loss; and, as Prebble found with Gilpinia this is essentially correct, for the average oven-dry weight of naked larvae only fell from 1.90 mg. to 1.81 mg. over 6 months of diapause.

Table 8.

Wt. of seed + larvae	1.1840 gms.	0.9930 gms.	1.1171 gms.	0.9747 gms.
Wt. of seed coats	0.9981 gms.	0.8365 gms.	0.9880 gms.	0.8168 gms.
Wt. of extracted larvae	0.1859 gms.	.1565 gms.	0.1831 gms.	0.1579 gms.
Larval Wt. as % Gross Wt.	15.7%	15.7%	15.6%	16.2%

Average % larval Wt. of Gross Wt. = 15.8%.

To demonstrate the efficient H_2O conservation of the micro-climate whole seeds, empty seed-coats and naked larvae were exposed at 60°F and R.H. 5% (S.D. 13.0 mm.). The water loss from the whole seeds was greatest in the first two days but after losing 6.9% of their original weight in 19 days they lost weight imperceptibly. Subsequent studies on the water contents of the seed coats and contained larvae of these 'whole' seeds showed that the water content of the testas fell from 57.7% to 51.9%. Naked larvae, similarly exposed, experienced a loss of 14.4% of their original weight their final water-content being 52.0%. Empty seed-coats lost 7.6% of their weight, their water-content was reduced from 12.7% to 5.7%. (See Tables 9 and 10.)

Part of the water loss from the whole seed related to moisture in the testa and part to the contained larvae. The exact proportion can be calculated as follows:-

The seed coat constitutes 84.2% of the combined weight of the seed + larva but we know from data above that the % loss of

initial/

initial weight of the testas was 7.6% after 34 days exposure to a Saturation Deficiency of 13.0 mm. Under the same conditions the loss of initial gross weight of seed + larva = 6.9%

∴ Loss from seed coats = 7.6 x 0.842

= 6.4% of initial gross Wt.

Hence Balance of gross weight loss attributable to contained larvae = 6.9 - 6.4

= 0.5% of initial gross Wt.

This loss in terms of initial larval weight = 0.5 ÷ .158

= 3.2%

Under the same conditions naked larvae lost 14.4% of their initial total weight which demonstrates the efficiency of the micro-climate in conserving water.

Table 9.

Weight Losses of Seeds and Larvae when exposed to S.D. of 13 mm.

Period of exposure.	Naked larvae		Empty Seed Coats		Full Seed	
	Wt. grams	% Loss of original Wt.	Wt. grams	% Loss of original Wt.	Wt. grams	% Loss of original Wt.
0	.5361	-	1.8583	-	3.2098	-
2 days	.5184	3.3	1.7357	6.6	3.0654	4.5
4 "	.5041	3.3	1.7301	6.9	3.0396	5.3
7 "	.4935	5.9	1.7245	7.2	3.0236	5.8
12 "	.4830	7.9	1.7198	7.4	3.0108	6.2
19 "	.4648	9.9	1.7171	7.6	2.9915	6.8
27 "	.4589	13.3	1.7171	7.6	2.9920	6.8
34 "	.4589	14.4	1.7171	7.6	2.9883	6.9

Prebble compared the live-weights of sawfly larvae extracted from cocoons following various periods of immersion in water

with/

with the weight of larvae from cocoons not so treated. But values obtained in this manner neglected differences in the original gross weight of the samples and so he divised a method of calculating these initial larval weights. His method has been adopted to follow the water-exchanges taking place in infested seed when it was kept in an environment of 100% R.H. for 4.5 days. (Table 11.)

Method (a) Av. Initial Gross Wt. of 1 seed = .04203 gms.

" " Larval Wt. = .04203 x 15.8%

= .00664 gms.

Method (b) Av. Gross Wt. (Seed + Larva) after exposure at 100% R.H. for 45 days = .04845 gms.

Ratio Larval / Gross Wt. after exposure = 11.3%

Original Larval Wt. prior to exposure of seed = .04845 x 11.3%

= .00547 gms.

The average of these two estimates .00605 gms. is the best approximation of the true larval weight at the beginning of the experiment. The final weight of the larvae, found by direct weighing following extraction from the seed, was .00463 gms. indicating that they were losing water despite the saturated environment outside the seed. It is thus apparent that the microclimate within the seed is kept below saturation otherwise the loss of water from the larvae could not take place. Maintenance of this microclimate is, however, acheived at the expense of the insect since, in dry air, the seed-coat merely delays the continuous loss of water from the larval tissues. Reference to Table 9. shows that the loss of water, even in dry conditions, becomes progressively less with increasing duration

of exposure./

of exposure. Thus when the water-content of the larva has fallen to 15.3% further loss is restricted by some physiological adoptation which, probably accounts for the fact that larvae can be extracted from the seed and will pupate succesfully following periods of up to 6 months exposure in Petri dishes in the laboratory.

Table 10.

	Live Wt.	Dry Wt. after 34 days at 13 mm. S.D.	Live Wt. Loss	% Initial H_2O Content	% Final H_2O Content
Naked Larvae	0.1565	0.0650	0.0173	58.5	53.2
	0.2174	0.0866	0.0407	60.2	50.9
	0.1622	0.0740	0.0080	54.4	52.0
			Mean Values	57.7	52.0
Empty Seed-Coats	0.8365	0.7350	0.0585	12.1	5.6
	0.9880	0.8589	0.0740	13.1	6.0
	1.0218	0.8900	0.0813	12.9	5.4
			Mean Values	12.7	5.7
Whole Seeds Larvae	0.1672	0.0799			52.2
	0.1989	0.0965		Mean	51.5
					51.9
Seed Coats	0.8542	0.7731			9.5
					8.3
	1.0129	0.9288		Mean	8.9

Table 11.

Initial Gross Wt. Seed (52)	2.1857 gms.	(50) 2.1045 gms.
Av. " " "	0.04203 gms.	0.02409 gms.
Final Gross Wt. Seed (52)	2.5194 gms.	(50) 2.4244 gms.
Av. " " "	0.04845 gms.	0.04845 gms.
Wt. of Larvae (52)	0.2410 gms.	(50) 0.2315 gms.
∴ Wt. per larvae	0.00463 gms.	0.00463 gms.
Dry Wt. larvae (52)	0.0990 gms.	(50) 0.0950 gms.
∴ Dry Wt. per larva	0.0019 gms.	0.0019 gms.

In view of the important function of the seed-coat in reducing loss of water and the findings of Prebble on sawfly cocoons where development was inhibited in all unsaturated environments but not entirely prevented even in the driest a number of Megastigmus larvae were exposed at different humidities.

The required humidities were obtained with the salts recommended by Shulov (1952) :- R.H. 100% Water; 91-90% KNO_3; 85-83% KCl; 74-71% NaCl; 53-50% $Ca(NO_3)_2$; 31-29% $CaCl_2$; 18% Saturated $ZnCl_2$; 0% H_2SO_4 (Density 1.84). These salts were placed in ground-glass stoppered bottles 4" x $1\frac{1}{2}$" and the larvae under test were extracted from the seed and placed (10 per tube) in tubes $1\frac{1}{2}$" x $\frac{1}{2}$", 5 of which were lowered gently into each larger vessel.

Table 12.

Relative Humidity.	No. Larvae exposed	No. Dead	% Mortality	No. pupated	% 2nd. Diapause	Av. No. days to adult
100	50	18	36.0	15	54.0	29
90-91	50	13	26.0	17	54.5	31
83-85	50	4	8.0	22	52.0	32
71-74	50	3	6.0	22	54.0	34
50-53	50	1	2.0	22	55.5	39
29-31	50	0	0	23	54.0	45
18	50	0	0	24	52.0	54
0	50	0	0	25	50.0	62 (only 2 developed)

These larvae had had 9 weeks cold-rest and the bottles were kept at a constant temperature of 77°F until emergence was complete.

These/

These results (Table 12.) show that the percentage of larvae that remain in diapause stays so constant as to suggest that the humidity of the environment has no controlling influence on this proportion. Mortality of the larvae on the other hand shows a progressive diminution with decrease of saturation, an effect which is probably correlated with the physical requirements of fungal and bacterial agents. It should be noticed that the length of the developmental period increases with the decrease in humidity suggesting that the shortage of water delays the complex physiological processes of that phase of development. Further only 2 out of 25 pupae matured at 0% Relative Humidity. In this connection it is interesting to examine (Table 13.) the % loss of water from the larvae within the seeds exposed to a low humidity calculated by the method adopted on Page 97. This method assumes that the ratio between larval weight and gross weight remains unchanged during the experiment. In actual fact however the original % ratio was 15.8 and after exposure to the dry conditions for 34 days the % ratio of larval weight / gross weight had risen to 16.3. In order to demonstrate the changes taking place in the water-relations of the larva it will be assumed that the mean ratio was 16.0.

Table 13.

Period of Exposure to 13 mm.	2 days	4 days	7 days	12 days	19 days	27 days	34 days
% changes of larval weight.	+6.3	+3.1	+2.0	0.0	-2.5	-2.5	- 2.8

These results indicate the rather interesting conclusion that the larvae actually gained in weight for the first week. This gain took place despite the gradual and continuous reduction in

gross/

gross weight of the whole seed. Such a gain in weight must have been in the form of water gained from the testa. This gain of water by larvae placed at a high temperature (77°F), following 9 weeks cold-rest, illustrated the need for some available water for successful pupation.

As a further demonstration that humidity does not influence the proportion of larvae remaining in diapause for more than one year 100 seeds after 9 weeks cold-rest were kept on soaked cotton-wool, 100 in a vessel at 100% R.H., and 100 kept in a dry tube - all these experimental lots were kept at 77°F until emergence was complete. Emergences were recorded daily and the mean date of maturation noted for each sample. Table 14.

Table 14

Treatment of Sample	No. Larvae	Larvae in 2nd. Diapause		No. days mean maturation
		Number	%	
Seeds kept in dry tube	90	47	53.2	13.1
Seeds at 100% R.H.	93	49	52.2	11.1
Seeds kept in contact with H_2O	89	48	53.8	11.0

We may therefore conclude that variations in humidity will have minimal effects on field populations breaking diapause.

Conclusions on diapause in Megastigmus.

Advantage was taken of the considerable collections of Douglas Fir seed made by the Forestry Commission in 1951 to calculate the mean % of prolonged diapause. in M. spermotrophus in that year for the various Conservancy Areas.

South East Conservancy	Mean % in 2nd. Diapause	19.9%
South West "	- .. -	15.9%
Eastern "	- .. -	16.1%
Northern "	- .. -	12.0%

North Wales Conservancy Mean % in 2nd. Diapause 16.0%

Data from the present studies produced the following results:-

	% in 2nd. Diapause	
	1950	1951
Bedgebury	22.7%	29.2%
Rosehaugh	51.3%	59.3%
Evanton	83.0%	44.2%

These figures suggest a number of tentative conclusions. The Forestry Commission data, which are computed from records of samples kept under the same conditions in one rearing room, when averaged out by Conservancy Areas showed a remarkable uniformity. These figures eliminate the effect of Spring weather by bringing samples from many areas into one room. The average figures therefore represent the combined effects of the room conditions and the genetic diapause component. That the latter exists is demonstrated by the data on temperature effects in an earlier section, however favourable these were to the 'break' of diapause, a proportion (approx. 10%) entered the prolonged rest.

In conclusion then, we may deduce that this small proportion is genetically prediposed to the long rest but that an additional proportion may not receive a sufficient environmental stimulus to emerge the first year. The figures obtained from Bedgebury and Ross-shire when compared would lead one to postulate that the lower Spring temperatures of the Northern county increase the percentage of larvae continuing diapause for a second year. The extraordinary high diapause figure at Evanton 1950 could be

explained/

explained on the following lines. The percentage of good seed in the crop was very high 42% and the percentage of good seed attacked by the Megastigmus females very low (15.0%). These conditions must have resulted in a large number of 'preferred' hosts and presumably a high oviposition rate. The classical work of Umeya (1926) showed that the environmental conditions affecting female Bombyx mori influenced the proportion of the larval offspring which entered diapause. Megastigmus larvae may be influenced similarly through the stimuli acting upon the females during oviposition.

Chapter VI.

Biology of Amblymerus? apicalis.

(a) Mating Behaviour

As with Megastigmus, adults of this species will attempt copulation within a few minutes of emergence from the seed. The male flies down on to the back of the female and stands with his wings raised as if preparatory to flight. He places his fore-feet on her head and the other legs on her thorax. Throughout the performance his antennae are kept in rapid vibration through a very small arc, so as to oscillate against those of the female, which are held sharply "elbowed" with the flagellum pendant. Periodically the male lowers his wings roof-wise over the female and vibrates them rapidly as if in flight. After two or three minutes display he steps quickly backwards bringing the tip of his abdomen in contact with the underside of that of the female. In captivity one pair were observed to be in display continuously for 10 minutes, copulation being attempted 12 times.

(b) Oviposition Behaviour

A most detailed account of oviposition in Habrocytus is given by Fulton(1933) and a similar process probably occurs in Amblymerus. The female has only been observed to oviposit in seed under laboratory conditions which were artificial. Females were kept in a large bell-jar illuminated by an electric bulb in close proximity. The seeds were examined with the antennae for some time before she raised her ovipositor vertically and drove it down through the steady pulsating rhythm of her body. An interesting form of "aggressive display" was observed if another

female/

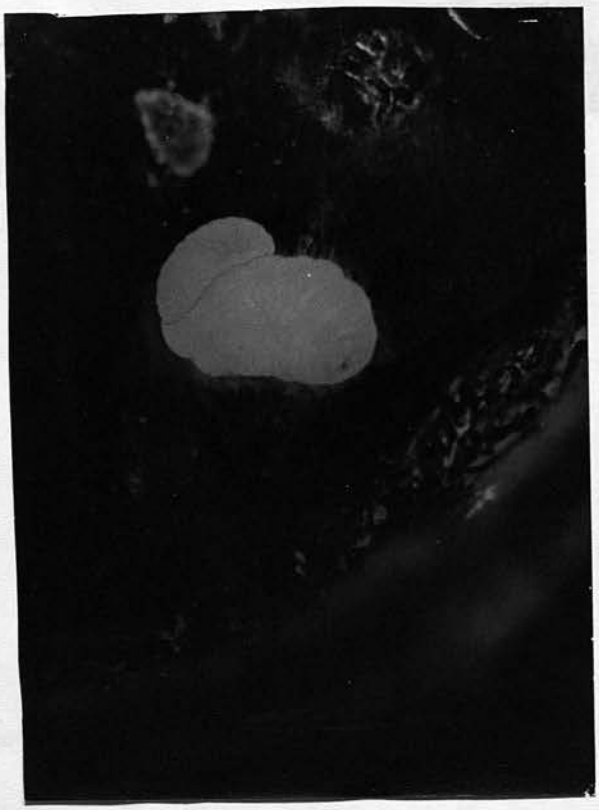
female approached her whilst her ovipositor was in situ, for without withdrawing, she would raise her wings from the folded position and elevate her antennae so that they were straight. The laying of one egg required from 5 - 7 minutes. The holes in the testa made by the ovipositor were easily visible owing to the reddish-brown area surrounding the puncture. In the case of the seeds used in the laboratory work more punctures were observed in the seed than eggs on the Megastigmus larvae therein. These extra holes were apparently used for feeding (c.f. next section).

In 1951 weekly collections of cones were made during the late summer and autumn to establish the time of egg-laying in the field. In that year the parasite laid its eggs during the last fortnight of October at Evanton. These collections, continued at intervals during the winter, revealed that, in the forest, the eggs do not hatch until the following Spring but if attacked seeds were brought indoors, hatching occurred within two days, even in January. Eggs laid in the laboratory in September hatched within 5 days, the resultant larvae entirely consuming their hosts in 33 days.

The eggs are apparently simply projected into the lumen of the seed and so fall on the Megastigmus larvae haphazardly. They have been found in all positions on the host and so far as can be ascertained they stick to the skin of the host simply by virtue of the slightly resinous deposit on the latter. Consequently they are often found free and unattached in the seed cavity.

(c) /

Mark caused by "feeding-tube" of Amblymerus in Douglas Fir Seed.



Amblymerus larva feeding on Megastigmus

(c) Feeding Habits

Adult Pteromalids are known to feed extensively on honey-dew, plant secretions etc. and in the present studies they were observed to feed readily on split-raisin. It has however often been observed that this carbohydrate diet is insufficient to meet the nutritional requirements of the female for egg production. In some species a protein diet is essential before oogenesis can begin. The body fluids of the host provide suitable food of the type and females have developed the habit of feeding on the fluids that exude from punctures made by the ovipositor. Some species, whose hosts remain in a secluded habitat e.g. cell, gall or cocoon, construct a "feeding-tube" extending from the puncture in the host to the outside of the wall of the cell. Fluids rise up this narrow tube by capillarity and the female Pteromalid uses her ligula to imbibe them.

Fulton (1933) has given a detailed account of the formation of this tube. Once the host has been punctured the ovipositor is withdrawn until only the tip penetrates the seed coat; a clear viscid fluid oozes from it which is twisted and drawn out downwards by the ovipositor, fresh material being added until the tube reaches the host.

In Amblymerus this tube is made of a fluid which hardens into a reddy-brown crystaline material, a small extension of which appears on the outer surface of the seed in the form of a raised rim. Feeding periods of the females at these punctures lasted about 10 minutes.

Flanders (1935) made observations on several Pteromalids and showed that when the ovarian follicles reach a certain stage

of development/

of development a change occurs in the food habits of the female, from carbohydrates to protein diet. After the beginning of egg deposition, a further amount of carbohydrate appears to be needed in addition to the host fluids. If environmental conditions inhibit oviposition, the ovarian follicles and the eggs disintegrate and are absorbed, the parasite reverting to a purely carbohydrate diet. A period of 'phasic castration' follows which may last as long as 9 months, the end of the period apparently being synchronised with the appearance of the susceptible stage of the host. The newly emerged parasites possess ovarioles well filled with primary oogonia and oocytes with their attendant nurse-cells, the nutrutive chamber of each egg-follicle always being larger than the oocyte chamber. The feeding by the parasite on the host fluids occurs when the oocyte chamber of one of the follicles equals or exceeds the nutritive chamber.

Studies on oocyte formation in Amblymerus were made by rearing males and females upon (1) sugar solution only and (2) sugar solution and seed infested with Megastigmus larvae. Females were removed from these trials every few days and dissected for examination of the ovaries.

From these observations several important details emerged. Firstly newly hatched females showed no differentiation of ovariole contents, until 5 or 6 days old the ovarioles were full of dense protoplasm. Between the 6th and 10th days differentiation into oocytes and nurse-cells occurred although in those females fed only on carbohydrates the eggs did not develop further. Those fed on protein as well (host larvae) contained

ovarioles/

ovarioles with at least one ripe full-sized egg by the 13th - 16th day. Under the conditions of these experiments the females would not oviposit in the seed but although oviposition was prevented the ripe eggs were not reabsorbed as found by Flanders. Females up to 60 days old contained as many as 3 ripe eggs in each of their 6 ovarioles but although these eggs were 'normal' in outline their contents had shrunk so as to appear as a ribbon-like band along the central axis of the egg from the 18th day onwards.

These laboratory bred females seldom had more than 3 eggs per ovariole at one time but field collected material (Oct. 11-16th, 1952) contained 6 eggs per ovariole with often 2 apparently "ripe". This evidence suggests a fecudity of at least 40 eggs per female.

(d) Longevity.

Adults of Amblymerus lived for much longer periods than Megastigmus, if kept under the same laboratory conditions. The average duration of life was 49.4 days for males and 65.9 days for females. The maximum periods observed were 60 days in a male and 80 days in a female. (Observations made on 25 specimens of each sex).

As the eggs are not laid until late October in the North of Scotland where the mean temperature would be considerably below the 60°F of the laboratory it is probable that they live for considerable periods in the forest. From an analysis of laboratory rearings and assuming that Amblymerus is affected similarly to Megastigmus by the congenial laboratory conditions it can be estimated that they appear in the forest during September.

No case/

No cases of overwintering by the adults in the cones has been observed.

(e) Field Activity of Adults

The most important feature of the life-history of this parasite requiring elucidation was whether or not the females would seek out the seeds infested by Megastigmus after they had been shed from the cone. If not, it was feasible that under certain conditions a proportion of the host larval population would be immune from attack.

In order to show whether this was the case a number of trials were set up in 1952 at Evanton. 8 lots of 10 cones infested by Megastigmus were cut from the tree and placed on the ground below the trees. From 4 of these lots of cones all the seeds were extracted by dissection and left in heaps. None of the host larvae in seeds placed on the ground in this way were parasitized nor were larvae in those cones blown to the ground by early autumn gales. Some cones on the ground were covered with "Sticktite" but no Amblymerus were trapped therein. A small "propeller" suction-trap driven from a 12-volt car battery was run for 4 hours at a time over other piles of cones without result. Two trees bearing 50-60 cones were felled in September the crowns remaining untouched throughout the oviposition period of Amblymerus in late October. No larvae in these cones were attacked.

When however the suction-trap was operated in the trees, at about 15'-20', near groups of cones female Amblymerus were frequently caught. Due to the rather damp situation in which the Douglas Fir plantations grow at Evanton, it was noticeable,

that/

that at the time Amblymerus eggs were first found in naturally-shed seed some cones inside the wood showed little sign of opening. Examination of some of these cones revealed that no parasite eggs had been laid but that during a spell of fine sunny weather when the scales began to open female parasites crawled beneath.

20 cones still tightly closed were taken and 10 dissected to show that no parasite eggs had been laid on the host larvae therein - the rest were opened with dry heat and tied on the trees next day. After 24 hours they were dissected to reveal that a number of Amblymerus eggs had been laid.

From this data it is evident that Amblymerus is unable to attack its host until the cone-scales separate and allow the female access to the seed. Thus it is feasible to postulate that a situation could arise in which the flight period of the parasite failed to overlap that of cone-opening. Reference to the previous sections however, where the long life of the adult females together with the delayed ripening of the ovarioles are mentioned, suggests that such a lack of synchronization is unlikely. A period of extremely low humidity, causing an exceptionally rapid seed-fall, could lower the parasitization if the parasite females had too short a time for oviposition. On the available evidence it would appear that Amblymerus, like Pimpla ruficollis. Grav. (a parasite of Evetria buoliana Schiff), is attracted to the host habitat before the stimulus to search and oviposit is manifested.

(f) Diapause

No experiments were conducted on the conditions affecting diapause in this species through lack of sufficient material

but/

but in the field the following data were obtained.

		Diapause in Amblymerus	Diapause in Megastigmus
Rosehaugh	1951	62.7%	51.3%
	1952	54.3%	59.3%
Evanton	1951	39.3%	83.0%
	1952	49.1%	44.2%

These figures suggest that, in general, the proportions of host and parasite undergoing diapause are similar but that occasionally, as in 1951 at Evanton, a considerable difference may occur. The only direct evidence on the factors influencing diapause is the difference between the values obtained from samples of seed, from the same trees, kept under different conditions. Lot A was kept in the laboratory for 7 months after receipt at a mean temperature of about 60°F. Lot B was kept in a greenhouse for a similar period where it was subjected to extremes ranging from 25°F to 85°F with the mean about 55°F. Lot C was transferred from the greenhouse to the laboratory just before parasite emergence began. The parasites in these samples had an extended diapause as follows, Lot A 42%, Lot B 54%, Lot C 80%. It is possible that the higher % diapause in Lots B and C was due to the lower quantity of heat in terms of day-degrees experienced by them. It would appear that the amount of heat experienced following the winter-rest is more important than the degree of cold during this rest. Lots B and C experienced more cold than A and yet the difference in % diapause B and C is greater than that between B and A.

(g) Sex Ratio

From all the parasite rearings made 935 males and 600 females were/

were obtained with a ratio of 1 : 1.6.

(h) Relative emergence periods of host and parasite.

Trägårdh (1918) put forward the suggestion that a certain relation existed between the emergence of the host and its parasites so that parasitic species with emergence peaks grouped around that of a phytophagous species could be safely concluded to be parasites of the latter. Reference to Fig. (58) shows that in the parasite-host relationship under discussion, alterations in the environment, can produce marked variations in the intervals between peaks of emergence of host and parasite. Referring to the divisions of seed lots into A. B. and C as in the Section on "Diapause in Amblymerus" we find that the intervals between these peaks of emergence are as follows:- Lot A 3 weeks Lot B. 5 weeks, and Lot C. $9\frac{1}{2}$ weeks. These discrepances could easily 'mask' relationships such as that envisaged by Trägårdh for the fauna of cones but even more important as suggested by Barnes (1930) could upset the synchronization of parasite and host. Barnes commented that " a possible cause of sudden great fluctuations in the degree of parasitism from one year to another may be due to alterations in the relative emergence - times of parasite and host which itself may be due to different effects of cold or heat on the parasite and host". In the case under discussion however the host larvae are ready for parasitization as early as mid-July and the only factor preventing oviposition by the parasites is the unopened cones, The considerable longevity of the female parasites should normally enable them to be active at the time of delayed cone-opening even in a year of "early" parasite emergence.

Chapter VII

Other Insects found within Douglas Fir Cones.

Anogmus ? strobilorum. Thoms. was reared from Megastigmus infested seed at Avoch and Evanton, Ross-shire, Mortimer Forest, Hereford and the New Forest. In the laboratory during 1952 an egg, mistaken for that of Amblymerus, found on a Megastigmus larva developed, after consuming its host, into a female Anogmus. Hitherto the species has been regarded as a parasite of various midges infesting cones of coniferous trees but throughout the work no Cecidomyidae were encountered in Douglas Fir cones. Anogmus strobilorum was not sufficiently numerous to be considered a useful parasite of Megastigmus.

The Pteromalid of genus Trichomalus near T. sunides and 2 Braconids Diplazon (Syrphoctonus) biguttatus Gr. and a Syrphoctonus sp. of the pictus group were reared from seed of Douglas Fir, infested with Megastigmus, at Evanton and Mortimer Forest. Larvae of these species were not observed feeding on Megastigmus larvae but as the seed was cleaned of other material before being placed in clean tubes the evidence indicates that at least they developed within the seeds. At Alice Holt these Bracomids were obtained in the same manner from other Douglas seed so that we may assume that they have other hosts than the Syrphid larvae with which they are usually associated.

Numerous other insects have been reared from cones of Douglas Fir but are regarded merely as hibernating therein:-

Aphideita obliterata L. Exochomus quadripustulatus L.	Coccinellidae
Rhynchaenus fagi. L. Strophosomus coryli. L. (= melanogrammus . Forst.)	Rhynchophora

Elatophilus nigricornis. Zett. - [redacted]. Anthocoridae

Necremnus leucarthrus. Nees. - Eulophidae.

Unidentified Amblymerus spp. other than A. apicalis

- Pteromalid.

Chapter VIII

The Bionomics of Megastigmus spermotrophus and its principal parasite.

Section (a)

Natural Control of an Insect Population

The literature on this general aspect of bionomics has reached considerable proportions so that the detailed review by Solomon(1939) is invaluable. From this study of previous work he drew a number of fundamental conclusions.

Amongst them was the conception that control is generally due mainly to physical factors in environments less favourable to life, where density is low; whilst biotic factors are important chiefly in physically favourable environments where density is high. Earlier Howard and Fiske (1911) concluded that parasites were the predominant unfavourable factor at moderate densities, disease when the insects had reached a density far beyond the average level and famine at the very highest levels. MacLagan and Dunn(1935) had suggested that natural populations are automatically checked by density effects(such as depression of reproduction by overcrowding) when all other inhibiting factors have failed. Solomon also comments that under crowded conditions, the mutual interference with feeding, mating and oviposition and the metabolic effects of continued stimulation, tend to reduce the output of fertile eggs,rate of development and longevity in animals.

Smith(1935) was the first to recognize the

the invaluable distinction between what he termed density-dependent mortality factors, which destroy a proportion of the population which proportion increases as the density increases, and density-independent mortality factors, whose effect is not related to population density. He considered the latter group mainly climatic, whilst the density-dependent factors included natural enemies, disease organisms, food-supply, space and protective niches(the last three being included on the grounds that when in limited supply they cause competition). Smith and Thompson(1939) recognized that climate can operate quantitatively in much the same way as is characteristic of biotic factors, i.e. it destroys a % which increases with density. It is probable that this occurs through the existence of protective niches in the environment. which are limited in number. Individuals in excess of this number cannot therefore attain these niches and are destroyed by unfavourable climate. In this connection it is interesting that MacLagan (1932) showed that no one set of conditions provides the optima for all the physiological processes of Smynthurus viridis so that, that insect is never precisely adjusted to its environment.

Solomon observed that density relationships may operate only above or below a certain threshold of density or they may be in force at all densities. He distinguished between concurrent density-relationships where the intensity of action rises as density increases and inverse density-relationships (insufficient

meeting of sexes Varley (1947) where the intensity of action falls as density increases. He stated that a fundamental reason for all types of density-dependent actions is the limited capacity of the environment to maintain large numbers of the species concerned, so that suppression by enemies is countered to some extent by density effects among the enemies. It is known that parasites suffer a reduction in their reproductive rate at high density Flanders (1935). Such effects would be minimal at high host density but if the hosts were much reduced in numbers so as to occupy localized "pockets", the parasites might become overcrowded through shortage of food or hosts. Such reciprocal reaction was considered by Varley(1947) to be another type of controlling factor called a delayed density-dependent factor.

The contributions of Nicholson (1933) and Nicholson and Bailey(1935) were mainly mathematical treatises but they formulated particularly interesting concepts of control mechanisms the most simple of which Varley (1947) has attempted to utilise in an analysis of a practical problem. Thompson (1939) has criticised Nicholson's theories but as Varley points out has based his criticism on a misunderstanding of that workers use of the term "random". Thompson argues that search cannot be random since parasites search for definite host species to attack. But by random Nicholson and Bailey meant a search for the particular host species in which the rate of discovery of hosts at any instant was proportional to the

product of the population densities of the searching parasites and the undiscovered hosts.

Nicholson considered it especially important to grasp the concept of "balance" in animal populations and he used a balloon as a simple simile, saying " the the balance of animal populations is similar to that of a balloon acted upon by the changing temperatures of night and day. Such a balloon rises and falls in relation to the change of temperature, for this varies the volume of the balloon and the density of the surrounding air. The balloon is continually in a state of tending towards a position of stationary balance but continues to rise and fall because the position of stationary balance is changing all the time". He drew attention to Holdaway's (1932) experimental study on Tribolium confusum which demonstrated that it is the interaction of the insects themselves which produces balance and so limits density, while physical factors, by modifying this interaction, influence the position at which the insects themselves limit their population. He examined critically the theories of control put forward by Bodenheimer(1938) and decided that if an attempt were made to assess the relative importance of the various factors known to influence a population no reliance could be placed upon the proportions destroyed by each. Indeed it was necessary to find which of the factors were influenced, and how readily, by changes in the density of the animals. Thompson (1928) had pointed out that the type of data usually collected in parasitological work does not

give an accurate estimate of the numerical variation of a parasitic species since they only measure apparent and not real mortality. The mode of control changes with development of the host, different factors acting at different stages, so that the importance of a factor cannot be evaluated simply by the % of hosts which it kills. The real significance of a controlling factor depends , rather upon the fraction of the population for the destruction of which it is indispensable, i.e. the % reduction due to a factor over and above that which it is calculated other factors would have produced without it.

Bess(1945) estimated for each factor the % by which it reduces the surviving population pointing out that in one generation of a fecund species a kill of 5% of the original population may be unimportant if 50% have been killed by other factors but very important if 90% have previously been killed. He introduced the concept of the mortality survival ratio as a measure of the relative effect of the mortality on the survival population. This ratio, being the quotient of the number, or %, of insects killed at any stage divided by the number,or %, that survived, represents the relative reduction per individual survivor. If expressed as a % it represents the % increase in the survival population which has been prevented by the mortality. He concluded that the relative reduction values of the different mortality factors during one generation do not represent their regulative value but

would be useful guides thereto when studied over a series of years at different population densities. Smith(1938) pointed out that in order to be effective a parasite must have the ability to find and destroy surplus progeny of its host at low host densities. He drew the conclusions that searching ability was of prime importance outranking reproductive capacity.

Nicholson(1933) observes that generally speaking, animals appear to be limited in density, either directly or indirectly, by the difficulty which they experience in finding the things they require for existence, or by the ease with which they are found by natural enemies. He deduces from this that searching among animals is important and that provided this property is random it is capable of simple analysis. Varley (1941) showed that the searching by parasite populations for their hosts is not always random.He concluded however that the exceptions to random searching are all small discrepancies in spatial distribution and that within limited areas the theories are likely to be accurate as a first approximation, unless host or parasite population densities are very low or uneven. Nicholson went on to suggest that the area searched could be measured by (a) <u>area traversed</u> or the total amount of searching done and (b) by the <u>area covered</u> representing the area within which objects had been successfully sought and found. On this basis Nicholson and Bailey(1935) produced their "competition-curve" which demonstrated that as the area traversed increases there is a progressive diminution in the rate of

increase in the area covered.

The area effectively traversed by an average individual during its lifetime was referred to by Nicholson as the area of discovery of the species under given conditions. Its value is determined by the properties of the searching animals and partly by the properties of the objects sought. It is therefore dependent upon the movement and keenness of the senses of the average searching individual and also upon the movement, size, appearance and smell etc: of the prey. Thus, under given conditions, a species will have a different area of discovery for each kind of object sought. The value of the area of discovery defines the efficiency of the species in discovering and utilizing objects of a given kind under given conditions and determines the density of animals necessary in order to cause any given degree of intraspecific competition. It is important to recognize that climatic conditions and other environmental factors play their part in determining the value of the area of discovery by influencing the activity of the insect.

Further increase in a population is prevented when all the surplus animals are destroyed so that the population is in a state of balance with its environment. When a population maintains its density from one generation to the next under constant conditions Nicholson speaks of a steady state and terms the population density in this condition of balance as the Steady density.

The formulae evolved by Nicholson and Bailey(1935)

were concerned with discontinuous generations i.e. a definite succession of generations occurred, all the parasite eggs were laid at the same time and all the hosts reached the vulnerable stage at the same time. These formulae produced a number of definite conclusions:-

1) The power of increase of a host species determines what fraction of the hosts the parasite must destroy in the steady state and so determines the fraction of the environment which the parasite must cover. Hence there is only one density at which parasites, with a given area of discovery, can exactly cover a given portion of the environment, so [redacted] we may conclude that the steady density of a parasite species depends upon its area of discovery and the proportion of hosts it is required to destroy in the steady state.

2) The steady density of the host species and that of the parasite vary inversely as the area of discovery of the parasite.

3) Reducing the power of increase of a host species decreases the initial steady density and increases the final steady density of the host; it also decreases the steady density of the parasite.

4) According to whether a destructive environmental factor operates before, after, or at the same time as a given parasite species, both the initial and final steady density of the host species are respectively lower than, higher than, or the same as they would be if the parasite were alone responsible for destroying the surplus hosts.

Nicholson also observed that violent fluctuations in host numbers tend to disorganize natural control and that sometimes a population escapes completely from one or several of its important controlling agents. This occurs because the hosts so outnumber the parasite that the latter is unable to attack all the hosts found. Such a phenomenon is referred to as release and it is obviously more common where control is dominated by one or two key factors. Thompson(1939) remarked that since it is agreed that "balance" in the sense of stability or oscillation about a mean value is at least approximately realised in Nature, it should be included in any study of the interaction of populations.

As a result of this survey of the present conceptions of natural control in insect populations it can be deduced that at present it is generally considered that controlling processes are the immediate determinants of density. But the physical environment is the ultimate determinant for it influences the controlling processes besides determining which controlling agents can be present.

Section (b)

The Census at the Bedgebury National Pinetum, Kent.

The studies at Bedgebury were conducted in the collection of Douglas Firs Pseudotsuga taxifolia which included both the varieties glauca and douglasii. The 44 trees grow in very open fashion over about an acre of ground and apart from two 100 foot

specimens their average height is about 40 feet. The group was relatively isolated from others of the species - a few individuals grew within ½ mile and a small young plantation was situated about 1½ miles away.

The small number of trees involved made possible a complete count of all the cones. This was carried out in June of each year when, with the aid of binocculars, cones of both the current and previous years were counted by two observers. If their estimates differed the mean was taken as the correct total for the tree. These totals enabled the number of host units available to Megastigmus in the current year, and also the number of "last year's" cones which had fallen to the ground during the winter, to be known. This latter estimate was checked by searching the ground below each tree for fallen cones. Such fallen cones which had formed part of the most recent crop were recognizable by their light brown colour compared with the deeper brown of those which had fallen in earlier years. In addition, the resin of the most recent cones was a rich wine colour but in older cones it darkened noticeably.

The number of scales per cone and hence the average number of seeds produced per cone were estimated from samples of about 30 cones each year. In the case of the cones of the current year all the seed embryos were extracted from the samples and viewed through a binocular microscope with transmitted light when the eggs, and/or larvae, were clearly visible for direct counting. Even at that early stage of cone

development a number of embryos showed signs of shrinkage and drying out; during the summer further seeds were affected similarly, killing any larvae therein. To assess this mortality factor seeds were collected each autumn before seed-fall and the seeds dissected to determine the proportion shrunken. In addition cones were kept overwinter to obtain data on larval and pupal mortality as well as emergence and sex-ratio. Such cones were kept in muslin-covered trays in the forest.

As a high proportion of the seed is shed from the cones during autumn and so becomes liable to the predations of mice and other rodents samples of litter 1 yard square were taken each year and examined for seeds. These samples removed the top 2" of litter or all the material to the soil surface depending upon the depth of the litter. Special care was taken to ensure that all portions of partially eaten seeds were found in such samples.

In any study of bionomics it is essential to evaluate the size of the population change from one generation to the next. It is possible to view such changes as a factor given by the product ;-

Fecundity x Proportion of ♀♀ x Fraction of eggs becoming adult

Each of these quantities will be evaluated in the subsequent discussion.

Section (c)

Factors affecting survival of eggs, larvae and pupae of Megastigmus.

(i) Egg Mortality.

When egg development proceeds normally the yolk shrinks away from the chorion at the ends so as to become elongate-oval in shape. Later the blastoderm shows as a transparent layer but as the shape of the larva becomes discernible this distinction disappears.

Of 970 eggs examined during the survey only two were abnormal. The yolk appeared full of large oil globules apparently caused by a break-down of the contents. It was considered therefore that egg mortality was sufficiently small, during the survey, to be neglected in the calculations.

(ii) Larval Mortality

Throughout the investigations only one case has been observed where two adults completed their development in the same seed so that it is practically certain that when the seeds contain more than one egg only one larva normally survives to maturity. It is possible that in such cases all the larvae would die from starvation but such a situation was not observed in all the hundreds of dissections made. The following observation throws additional evidence upon the subject. A group of cones were selected growing close together upon a branch so that they had probably received the same attention from female Megastigmus. Some were cut down in late June 1952 and dissected for eggs whilst the rest (12) were allowed to grow on until September under muslin bags.

The sleeved cones contained 219 "good" seeds of which 208 contained 5th. instar larvae. The cones dissected in early summer were infected with eggs at the rate of 95% of the good seed, a proportion which suggested that the 219 good seeds should have contained 208 larvae. This exact correspondence occurred despite the fact that 17% of the seeds examined in spring contained more than one egg. The inference, therefore, is that in all cases where multiparasitism occurs all but one of the larvae perish at an early stage.

This form of larval mortality will be referred to as density-mortality. It is calculated simply by summing the total number of eggs laid and in all cases of multiparasitism deducting as "mortality" all eggs in excess of one. Thus in 1950 2.2% of all seeds infested contained two eggs. Only one of these was destined to survive so that the density-mortality was 2.2%.

	1950	1951	1952	1953
% Larval Density-Mortality	2.2	14.0	38.6	44.3

As commented upon elsewhere a high proportion of the seed of Douglas Fir shrinks naturally during development so that in the autumn the lumen of the seed is empty apart from the white shrivelled endosperm. This shrinkage has reached an incipient stage about the time of oviposition so that it is possible to record the number of eggs laid therein. All larvae hatching in such an environment die of

starvation within a few weeks so that we may refer to this form of larval mortality as Shrinkage-Starvation Mortality.

That ♀ Megastigmus "prefer" seeds in which shrinkage is not present is shown by the fact that the proportion of these unsuitable seeds attacked increases when the cone crop is low.

TABLE 15

Year	1950	1951	1952	1953
Number of cones available for oviposition	9396	4143	2094	9348
% Shrunken Seed Infested	Nil	37.6	48.6	17.6

TABLE 16.

	1950	1951	1952	1953
Number of eggs per seed laid in good seed				
1	92	523	164	330
2	2	58	90	259
3	0	15	25	82
4	0	9	12	48
5	0	0	3	0
6	0	0	2	0
Total infested seed examined	94	605	296	719
Number of eggs per seed laid in shrunken seed				
1	0	187	26	168
2	0	6	9	28
3	0	5	1	0
Total infested seed examined	0	198	36	196

Thus discounting the density-mortality that would have occurred where more than one egg per seed was laid the "shrinkage starvation mortality" for 1952 is derived as follows :-

82.9% of the total seeds were shrunk but only 48.6% of these shrunken seeds were infested therefore $\frac{82.9 \times 48.6}{100} = 40.3\%$ of seeds were both shrunken and infested. As the number of eggs laid per 100 seeds was 76.2 (see Page 140) the proportion of the eggs destined to die by this form of mortality was $\frac{40.3 \times 100}{76.2} = 52.9\%$.

TABLE 17.

Year	1950	1951	1952	1953
% Shrinkage-Starvation Mortality	Nil	16.4	52.9	28.1

A third type of larval mortality which occurred regularly in the 4th. and 5th. instars was probably due to disease. No fungal hyphae were present but most of the infected larvae were shrunken, dark yellow in colour, dry and very hard. A few were soft and very dark brown suggesting that death may have been the result of bacterial decay.

These diseased larvae were counted directly and the % mortality calculated on the basis of all normal 5th. instar larvae present a few weeks before emergence.

Disease Mortality %	1951	1952	1953
	7.4	2.0	1.6

(iii) Pupal Mortality.

A few pupae failed to yeild adults and were found dry and shrivelled. The percentage pupal mortalities were :-

1951	1952	1953
3.2	0.8	Nil

(iv) Mortality due to Mice.

Many of the seeds which were shed from the cones

and fell to the ground were found, the following Spring, to be damaged by large gaping holes along one side or else only fragments of the testas were recovered. Those that had contained Megastigmus larvae were regnizable by the dead-white lining of the seed -coat which, although a separate layer, seemed to remain in situ for long periods. In shrunken seeds this layer formed a shrunken envelope to the shrivelled endosperm.

Evidence that mice were responsible for this damage is largely based on feeding experiments in which both Bank Voles Cleithrionomys glareolus and Long-Tailed Field Mice Apodemus sylvaticus, were fed with Douglas Fir seed and produced the characteristic damage. Such damage is always confined to shed seed- seed in cones on the ground was never affected. Further evidence was furnished by setting out lots of Douglas Fir seeds in wire cages about 8" x 6" x 4" the mesh of which was (a) $\frac{1}{2}$" to exclude mice and birds (b) $1\frac{1}{2}$" to exclude birds only and (c) simply a wire frame to allow access by both.

These trials (Table 18) serve to indicate that (i) Bird damage was negligible (ii) that damage by insects which could get through the small mesh was nil. (See also Table 20).

It is also of interest to record that in no case during the many trials conducted were Silver Fir seeds attacked by mice which seems to indicate that an important control factor is largely lacking in the case of M. pinus. Although perhaps not

completely so as damaged Abies seed was found in the Novar Forest in 1952.

TABLE 18

	Seed Damaged	Seed Missing	Survival
Mice and Birds excluded	0	0	100
	0	0	100
	0	0	100
	0	0	100
	0	0	100
	0	0	100
Birds Excluded	25	53	22
	23	51	26
	21	47	32
	42	50	8
	29	59	12
	8	92	0
Both Birds and Mice admitted	20	66	14
	18	70	12
	28	36	36
	74	16	10
	15	85	0
	48	37	15

Mean Survival when both Birds and Mice excluded = 100%

Mean Survival when Birds alone excluded = 16.7%

Mean Survival when both admitted = 14.5%

TABLE 19

	1951	1952	1953
% Seed damaged by mice	30.4	31.4	20.2
% Megastigmus infested seed damaged by mice	68.8	60.0	50.0

These figures take no account of seed carried off entire by the mice. Varley in his studies on Urophora found that the winter disappearance of the galls, largely due to mice, was 61.5% in addition to the 18.5% actually recovered damaged.

From Table.19. it is interesting to observe that

the % of previously infected seed found damaged is much higher than the values of % total seed damaged and % total seed infected would lead one to expect. There is, therefore, some evidence that infested seed is preferentially sought out by the rodents.

To obtain some indication of the proportion of seed carried off in addition to that found damaged a number of experiments were laid down. Sites were selected at random by marking every sixth tree along a diagonal through the wood. At the base of each tree so marked 100 seeds, minus their wings to prevent loss by wind, were placed and left for two months. After that time the litter was scraped up and examined for seed.

Reference to Table.20. indicates that there is a greater tendency for seed to be carried off whole, presumably to a store, during the late summer and winter.

Calculating the mean values on the whole year's results :-

% seed damaged	= 766/60	= 12.8
% seed missing	= 3853/60	= 64.2
% seed recovered whole	=	= 23.1

This value of 23% is probably too low for the % of naturally shed seed remaining undamaged during the winter as the rodents would more easily discover lots of 100 seeds than seeds indiscriminately scattered. However we can fairly safely assume that for every seed damaged 4 seeds will be carried off entire. It is

interesting that during trapping experiments in 1953 this relationship was found to hold good when comparing the number of seeds trapped daily per square foot with the number found in the litter between the traps in the spring.

Number of seeds trapped	390, 412, 389, 308.
Number of seeds found in same area of litter in spring.	70, 80, 76, 75.

Using this factor with the litter sampling results (Appendix 1)we can estimate the % loss of Megastigmus by rodents :-

1951

Seeds found damaged =69

Therefore seeds carried off = 276

Seeds found undamaged = 158

Hence revised total= 503

Therefore % loss due to mice = 58.6

1952

Seeds found damaged = 37

Therefore seeds carried off = 148

Seeds found undamaged = 81

Hence revised total = 266

Therefore % loss due to mice = 69.5

1953

Seeds found damaged = 18

Therefore seeds carried off = 72

Seeds found undamaged = 71

Hence revised total= 161

Therefore % loss due to mice = 55.9

Table 20.

Seed Placement Experiments

Period of Exposure	Damaged	Recovered Entire	Missing	
December - January	6	1	93	
	1	0	99	
	4	0	96	% Recovered
	0	0	100	15.8
	11	7	82	
	14	12	74	% Damaged
	29	22	49	8.3
	10	5	85	
	6	10	84	
	2	18	80	
February-March	2	2	96	
	25	22	53	
	23	26	51	% Recovered
	21	32	47	31.9
	36	5	59	
	20	2	78	% Damaged
	1	5	94	16.9
	8	27	65	
	15	16	69	
	18	13	69	
April-June	12	0	88	
	52	24	24	
	20	14	66	% Recovered
	18	12	70	44.4
	28	36	36	
	4	52	44	% Damaged
	24	20	56	20.8
	19	28	53	
July - August	15	32	53	
	0	4	96	
	7	12	81	
	0	60	40	% Recovered
	0	15	85	28.6
	0	48	52	
	2	27	71	% Damaged
	0	32	68	1.3
	1	42	57	
	3	21	76	
September-October	0	12	88	
	6	11	83	
	1	85	14	% Recovered
	2	24	74	54.9
	7	80	13	
	10	67	23	% Damaged
	3	30	67	6.4
	5	50	45	
	8	41	51	
	10	39	51	
	12	58	30	

Period of Exposure	Damaged	Recovered Entire	Missing	
November-December	25	22	53	
	23	26	51	
	21	32	47	% Recovered 39.1
	42	8	50	
	29	12	59	
	8	0	92	% Damaged 22.9
	20	14	66	
	18	12	70	
	28	36	36	
	15	0	85	

During each of the two monthly periods in the above table lots of 100 seeds were placed in a wire-cage to exclude mice. At no time were seeds missing or damaged so that we may infer that the loss of seed in Table 20. was due to mice.

Section (d).

Fecundity.

As it was impossible to provide sufficient females with cones, under natural conditions, fecundity was not measurable directly so that recourse was made to Sachtlebens (1927) work in which he showed that so long as migration could be neglected the mean fecundity per female = $\frac{\text{No: eggs laid per unit area}}{\text{No; females emerged per unit area}}$.

Varley (1947) in his study on Orophora used a square metre as his unit of comparison but such a horizontal measure is unsuitable for cones growing upon trees. Hence in the present study "unit area" has been taken as 100 seeds. Such a reference is perfectly suited to the term "No: eggs per unit area" but it must be remembered that the females, in the year of oviposition, will have emerged from seed produced in the two previous years. Further, the number of cones

produced varies from year to year so that the number of females per 100 seeds must be calculated by estimating the actual number of females emerging each year.

Calculation of number of females available for oviposition in 1952 (Based on data in Appendix 1).

As the number of 1951 cones remaining on the trees in the spring of 1952 was 3571, each with 10.1 seeds, the number of seeds still on the trees was 36067. Of these 15.1% contained Megastigmus so that there were 5446 larvae in these cones. This total was reduced by the action of 3.0% larval mortality, 0.7% pupal mortality to 5246 larvae. Only 50.7% of these larvae emerge in the first year so that the number of larvae emerging as adults in 1952 was 2660.

The number of 1951 cones fallen to the ground over-winter was 572, each with 12.2 seeds, so that 6978 seeds remained in these cones. 10.8% contained Megastigmus giving a total of 740 larvae. These were reduced by 1% larval mortality and 1% pupal mortality to 726 larvae of which 90.8% emerged in 1952 giving a total of 659 adults.

The rest of the seed was shed from the cones during the winter. As there were 4143 cones each with 79 seeds the total seeds produced in 1951 were 327297 but from the two previous calculations we know that 43045 seeds remained in the cones so that the number shed was 284252. Of these only 15.2% or 43306 were good. 95% of this good seed was attacked by Megastigmus

and the larval population reduced by 2.0% larval mortality, 69.5% mice predation and 0.8% pupal mortality. Of the final larval population only 70.8% emerge in 1952 so that of the 43306 good seeds will yield 8661 adults (20.0%).

Therefore total number of adults emerging is 2660 + 659 + 8661 or 11980. The number of larvae overwintering until 1953 is 6204 made up of 2586 in cones on the trees, 67 in cones on the ground and 3551 in shed seed.

Results of whole census at Bedgebury.

	1951	1952	1953
Cones left on trees	8406	3571	N/A
Seeds ,, ,, ,,	52958	36067	,,
,, + Megastigmus	11969	5446	,,
Adults emerging in current year	8560	2660	;;
Adults emerging following year	3187	2586	,,
Cones fallen to ground	990	572	,,
Seeds ,, ,,	18909	6978	,,
,, + Megastigmus	4028	740	,,
Adults emerging in current year	2630	659	,,
Adults emerging following year	772	67	,,
% Good seed infected	98.0	95.0	83.8
Less larval mortality	90.8(7.4)	93.1(2.0)	82.3(1.6)
,, mice damage	28.6(68.6)	28.4(69.5)	36.3(55.9)
,, pupal mortality	27.7(3.2)	28.2(0.8)	36.3 (Nil)
% adults emerging in current year	20.8(75)	20.0(70.8)	26.4(72.7)
Total seeds shed	457128	284252	161238
,, ,, suitable for Megastigmus	59427	43306	27572
Number adults emerging in current year	12346	8661	728
Adults emerging next year	4115	3551	N/A

	1951	1952	1953
Total adults emerging in current year	23536	11980	728 [redacted]
Total larvae remaining in diapause till following year	8074	6204	N/A

It should be remembered that larvae remaining in diapause for a second year will be liable to a further reduction in numbers through mortality factors acting for a second period. Although mice do not attack seed within cones this may be discounted in the second year as the number of seeds remaining in the cones for so long will be very small. Hence the 8074 "1951" larvae will be further reduced by 2.0% larval mortality, 69.5% due to mice and 0.8% pupal mortality so that 2438 adults will have emerged in 1952. The corrected value for larvae diapausing from 1949 cannot be calculated through lack of data but as 1950 was a good"seed-year" it is reasonable to suppose that in 1949 the cone crop was about the same as that in 1951. It is therfore assumed that 1800 of them will have emerged as adults in 1951.

Therefore :-

	1951	1952	1953
Total No: adult Megastigmus emerging	25336	14418	3420
Proportion females	.60	.71	.48
Therefore number of females	15202	10237	1642
Number of young cones	4143	2094	9348
Number of seeds available for oviposition	327297	161238	678771
No: females/100 seeds	4.4	6.4	0.2

Calculation of number of eggs laid per 100 seeds

1952.

Shrunken Seeds 82.9	Good Seeds 17.1
48.6% attacked by Megastigmus	83.8% attacked
Therefore 40.3 seeds + eggs	14.3 seeds + eggs
72% with 1 egg = 29.0 eggs	55.4% with 1 egg = 7.9 eggs
25% ,, 2 ,, = 20.2 ,,	30.4% ,, 2 ,, = 8.6 ,,
2.8% ,, 3 ,, = 3.3 ,,	8.4% ,, 3 ,, = 3.6 ,,
52.5	4.0% ,, 4 ,, = 2.3 ,,
	1.0% ,, 5 ,, = 0.7 ,,
	0.7% ,, 6 ,, = 0.6 ,,
	23.7

TABLE 21

	1950	1951	1952	1953
Total eggs/100 seeds	29.7	51.6	76.2	28.8
Megastigmus ♀♀/100 seeds		4.6	6.4	0.2
Fecundity/female	?	11.2	11.9	144

Section(e)

Discussion of Results at Bedgebury.

It is instructive to analyse the results obtained by the method suggested by Bess(1945). He calculated the mortality-survival ratios for the various stages of an insect's development. When applying the formula it is important to recognize the fact that death due to disease and mice occurs at the same time so that, as shown by Bess, it is necessary to use the final survival % from all causes of mortality in the late larval instars. Example :- mortality/survival ratio

$m/s = \frac{\%\ \text{killed}}{\%\ \text{survived}} = \frac{68.6}{20.8} = 3.3$

TABLE 22

	1950		1951		1952		1953	
	%	m/s	%	m/s	%	m/s	%	m/s
Larval-density mortality(good seed only)	2.2	.002	16.0	.24	40.1	5.7	44.3	1.6
Shrinkage - starvation mortality	0	0	16.4	.24	52.9	7.6	28.1	1.0
Total early larval mortality	2.2	-	32.4	-	93.0	-	72.4	-
Larval mortality (Disease)	7.4	.35	2.0	.07	1.6	.04		
Pupal mortality (Disease)	3.2	.15	0.8	.03	0	0		
Mortality due to Mice	68.6	3.3	69.5	2.5	55.9	1.3		
Total 5th. instar and pupal mortality	79.2	-	72.3	-	57.5	-		

In the present study it is particularly useful to distinguish the early-larval mortality (affecting instars 1 to 4) from that of the 5th. and pupal instars. An error is inherent in the results owing to the fact that a proportion of the population is always in diapause for more than one year and so experiences a larger mortality in the late stages than has been used. This does not, however, invalidate a comparison of the effects of host-density on early and late larval mortality.

Bess showed that to sum two mortality/survival ratios A and B it is necessary to use the formula

Total = A + B + AB

TABLE 23

Summed Relative Reduction Factors.

	1950	1951	1952
Early -Larval Mortality	.002	.538	43.3
Late larval and Pupal ,,	5.67	2.87	1.39
Total Number of cones	9396	4143	2094

The total effects of the various reduction factors can also be expressed in terms of their Relative % Equivalents which indicate the % mortality which they would have been able to cause had they been capable of killing the same % of hosts, in the absence of other factors, as they did when the other factors are also operative.

$$\text{Relative \% Equivalent} = \frac{M/S}{M/S + 1} \times 100$$

TABLE 24

Relative % Equivalents

	1950	1951	1952	1953
Larval-density mortality	0.2	19.3	85.1	61.5
Shrinkage-starvation ,,	0	19.3	88.4	50.0
Larval Disease ,,	25.9	6.5	3.8	n/a
Pupal Disease Mortality	13.0	2.9	0	n/a
Mortality due to mice	76.7	71.5	56.5	n/a

Bearing in mind the increasing density per cone of the Megastigmus females from 1950-2 it is apparent that the early-larval mortality is strongly density-dependent. Varley(1947) concluded that, had such a factor been the only density-dependent process controlling Urophora, almost 100% of the Knapweed flowers would have been attacked. Such indeed is the situation with

Megastigmus where no parasites are active, for the late-larval mortality is not density-dependent.

The disease vectors decreased in effect in the lighter seed-years presumably because the density of 5th. instar larvae per tree was less with the result that the disease had less opportunity of spreading from host to host.

The decrease in the mortality due to mice probably occurred because the seed of Douglas Fir is not a "normal" diet for rodents but will apparently be consumed when the animals come across it. As the numbers of seed decrease their density on the ground will also decrease so that one would expect fewer to be discovered. The advent of a particularly severe winter would lead to a higher loss as the mice would search more intensively for seed once their usual diet could not be met.

It is evident that, once established in a plantation, Megastigmus is capable of destroying almost all the seed produced if no other factor than larval-density operates in a density-dependent fashion.

The only situation in which a fairly high proportion of the crop may escape infestation would arise when a good seed-year followed a number of poor years. In such an event the number of potentially good seeds could exceed the total fecundity of the Megastigmus population. From dissections of fertile females it is estimated that they are capable of laying at least 30-50 eggs(based on eggs in ovarioles). From Table 21. it is evident that if the density of females per cone is low

almost 150 eggs may be laid. This means that each female could attack all the good seed in 4-5 cones. Hence in order to have a proportion of the crop uninfested many more cones must be produced in the "good" seed-year than female Megastigmus emerge in that year. It should be remembered that if a high % of the population two years previous entered prolonged diapause a greater number of females would emerge in the current year than the size of the cone crop in the previous year would lead one to expect.

Under British conditions it is unusual for the % of good seed in the crop to exceed 50% so that assuming 100% infestation in the poor years about 40 larvae would develop in each cone. Late larval mortality and mice appear to account for at least 60% so that only 10 larvae will survive to maturity. Taking the proportion of females as .5, five females would emerge from each cone to attack the current crop. Therefore unless the cone crop is about 25x as great as that of the preceding years the chances are that most of the seed will still be infested. In many areas however the % of good seed is often as low as 15% so that emergent females would be capable of attacking as many as 15 cones.

As the cone crop borne by individual trees has been found to vary as much as 50-fold from year to year it is possible for the number of cones to exceed the egg supply of Megastigmus.

Section (f)

The Census at Rosehaugh.

The study took place at the Rosehaugh Estate, Avoch, Ross-shire where the Douglas Fir crop consists of a number of ornamental trees about 80' high and a plantation of about 3 acres of trees 70' tall. All were P.douglasii. The nature of this crop, especially the plantation where the closed canopy prevented the cones being visible from the ground, necessitated a different method of assessing the total cone crop from that adopted at Bedgebury. A number of trees were selected for cone-counts and the ratio between the crops on these trees taken as the ratio between the total cone crops for these years. The fact that oviposition by Megastigmus occurred in the North only a little later than in Kent prevented direct observations which would have thrown light on some of the anomalus data obtained in irregular visits. The site was visited in the spring and autumn of 1951 and 1952 to obtain litter samples and make cone counts. Seed was collected while falling from the cones and cones picked from the trees, and off the ground, for examination. To provide data on the growth of the insects throughout the year Mr. Patience of Avoch kindly sent cones at regular intervals. One of the most important factors about which figures were required was the proportion of the parasite and host larvae which overwintered more than once. These data were obtained by placing cones in gauze-covered tins

on the ground and leaving them thus exposed until emergence in the current year was complete when the seed was dissected.

The analysis of the material was carried out in the same manner as at Bedgebury. As fewer samples were taken the number of seeds retained by the cones overwinter were calculated by means of the data obtained in British Columbia by Garman(1951). Regular samples throughout the winter showed that as a broad approximation his figures held for seed release in Ross-shire. Hence for the purposes of the calculations to follow it has been assumed that 20% of the seed in each year remained in the cones and so escaped the depredations of mice.

The number of cones blown to the ground was ignored as the number was small and too difficult to determine with accuracy in dense plantations.

Section (g)

Census at Novar Estate, Evanton.

The studies were made in two plantations of Douglas fir adjacent to one another. One block consisted of 1½ acres of 80' trees the other ½ acre of trees 30-35' high.

The methods of sampling were the same as those employed at Avoch. Sampling of the cones for parasitization was facilitated by windblow in the autumn of 1952.

Section (h)

Analysis of the Results obtained at Rosehaugh.
(Based on data in Appendix 11)

As the total number of cones involved on the site was not determined calculations are based on 1000 cones borne in 1950.

Average number scales per cone = 40.4

Therefore total seeds produced = 81 x 1000 = 81000

But as only 32.1% of these seeds were good, and so suitable for oviposition, only 20775 larvae occurred. (79.9% good seed attacked).

48.2% of these larvae were however parasitized by Amblymerus so that in the late Autumn we had

10761 Megastigmus larvae

10014 Amblymerus larvae.

Following Garman's work (1951) 20% of the seed remains in the cones overwinter and so is not affected by rodents.

Therefore 2152 Megastigmus larvae and 2003 Amblymerus larvae were unattacked by mice.

But 8609 Megastigmus larvae and 8011 Amblymerus larvae were subject to 59.9% attack by rodents.

Therefore survivors =

3453 + 2152 = 5605 Megastigmus larvae

3212 + 2003 = 5215 Amblymerus larvae.

But late larval mortality of Megastigmus = 15.1%.

Therefore 4759 Megastigmus larvae survived in the Spring of 1951.

Late larval mortality of Amblymerus = 14.6%.

Therefore 4454 Amblymerus larvae survived in the

Spring of 1951.

However the proportion of larvae remaining in diapause for a second winter were:-

Megastigmus 51.3% Amblymerus 62.7%.

Therefore adults hatching in the Spring of 1951

Megastigmus	Amblymerus.
2318.	1661.

Larvae Overwintering again until 1952.

2441.	2793.
Sex Ratio 0.4	0.38

Therefore number of females emerging =

Megastigmus 927	Amblymerus 631.

The cone crop of 1951 was 0.11 that of 1950. Hence on the same area as that on which 1000 cones would have grown in 1950 there would, in 1951, have been 110 cones with 86 seeds in each .

Therefore total seeds produced = 9460 of which only 32.3% were good so that number of seeds available for oviposition was 3056 leaving 6404 shrunken.

As only 38.4% of the good seed was attacked the number of Megastigmus larvae would have been 1174.

From dissections of seed embryos it was established that all the seeds attacked contained only 1 egg each. But two out of 118 eggs were found in shrunken seed so that it is presumed that 1.7% of the 6404 shrunken seeds contained eggs.

Hence total eggs laid by Megastigmus = 1174 + 109
= 1283

51.1% of the 1174 Megastigmus larvae were parasitized by Amblymerus therefore in the late

autumn there were

574 Megastigmus larvae
600 Amblymerus ,,

Dissections showed that only one parasite egg was laid per host so that Number of Eggs laid by Amblymerus = 600

As 20% of the seeds remain within the cones

115 Megastigmus larvae and 120 Amblymerus larvae were immune from attacks by mice. The rest 459 host and 480 parasite larvae were subject to 82.1% rodent attack.

The number of larvae overwintering from 1950 must also be taken into account so that the total number of larvae liable to rodent attack is :-

Megastigmus 459 + 2441 = 2900

Amblymerus 480 + 2793 = 3273

Hence the numbers surviving attack were 519 Megastigmus larvae and 586 Amblymerus. To these we must add those remaining in seed within cones so that the total surviving populations were :-

Megastigmus 634 Amblymerus 706

Late Larval Mortality

6.3% 1.6%

Therefore larvae surviving in spring 1952

500 + 94 = 594 593 + 102 = 695

% larvae remaining in diapause for a second winter

59.3% 54.3%

Therefore number of adults emerging in spring 1952

297 + 94 = 391 322 + 102 = 424

Sex - Ratio

0.2 0.5

Therefore number of females emerging

Megastigmus 78

Amblymerus 212

The cone crop of 1952 was 0.76 of that in 1951

So there were 84 cones with 82.4 seeds each

Hence 6922 seeds were present of which 37.9% were good

Therefore 2624 good seeds were available for oviposition and eggs were laid in 51.9% of them.

Number of Megastigmus larvae = 1362

From dissections of seed embryos it was established that all the eggs were laid in good seed. But of 240 embryos examined 12 contained two eggs.

Hence Total no: eggs laid by Megastigmus = 1362 + 68

= 1430

Parasitism of these 1362 larvae reached 48.4% but as only 1 egg was observed on each host

Total no: eggs laid by Amblymerus = 659

Section (i)

Analysis of results at Evanton.(Based on data in Appendix 111)

Assuming once again a total of 1000 cones each with 85 seeds there were 85000 seeds of which 43.3% were sound and suitable for oviposition.

Therefore no: good seeds = 36805 of which 15.6% were attacked by Megastigmus so that no: larvae was 5742.

As 18.9% of these were parasitized there were, in the late autumn, 4657 Megastigmus and 1085 Amblymerus.

20% of the seeds remained in the cones so that 931 Megastigmus and 217 Amblymerus were unaffected by rodents whilst 3276 Megastigmus and 868 Amblymerus were subject to an 82.8% reduction by this factor.

Therefore surviving populations :-

Megastigmus = 1572

Amblymerus = 366

Late Larval Mortality

Megastigmus	Amblymerus
21.7%	0%

Larvae surviving in spring 1951

1231	366

% larvae entering extended diapause

83.0%	39.3%

Adults emerging

210	222

Sex-Ratio

0.62	0.49

Females emerging in spring 1951

130	109

The 1951 cone crop was 0.2 of that in 1950 Hence there were 200 cones with 69.8 seeds each on the area occupied by 1000 cones in 1950.

Therefore 13960 seeds of which 21.4% or 2988 were good. Of these 95.1% were attacked so that there were 2842 larvae.

Dissections of embryos showed that of 206 good seeds only one or 0.5% contained 2 eggs. Of 192 shrunken embryos 39(or 20.3%) contained eggs.

Therefore no: eggs laid by Megastigmus = 2842 + 14 + 2227
= 5083 eggs

Of the 2842 larvae 39.4% were parasitized so that in late autumn there were :-

1722 Megastigmus 1120 Amblymerus

Dissections of seed soon after oviposition by the parasite showed that of 81 host larvae attacked 6 contained two eggs, 3 three and 3 four.

Therefore no: eggs laid by Amblymerus = 1120 + 453
= 1573 eggs

As 20% of seed remains within cones 344 Megastigmus larvae and 224 Amblymerus larvae were unattacked by rodents whilst 1378 host and 896 parasite larvae were subject to a 88.6% reduction by this factor. But we also take account of those larvae overwintering from 1950 so that total populations subject to attack were :-

2399 Megastigmus 1040 Amblymerus

Survivors

611 343

Late Larval Mortality

2.9% 1.3%

Larvae surviving in spring of 1952

Megastigmus	Amblymerus
260 + 333 = 593	117 + 221 = 338

% larvae in extended diapause

44.2%	49.1%

Number adults emerging in spring 1952

149 + 333 = 482	60 + 221 = 281

Sex-Ratio

0.65	0.54

Number females emerging in spring 1952

313	152

Cone crop of 1952 0.2 of that of 1951

Therefore 40 cones with 76 seeds each giving a total of 3040 seeds of which 19.7% or 599 were good.

69.7% of these were attacked by Megastigmus sothat Megastigmus larval population was 418.

Dissections showed that all eggs were laid in good seed but that of 169 seeds 8 contained two eggs.

Total no: eggs laid by Megastigmus = 437 eggs

Parasitism of these 418 larvae was 63.2% and as only 1 egg was observed on each host

No: eggs laid by Amblymerus = 264

TABLE 25

Synopsis of essentail data derived from census results at Evanton and Rosehaugh.

	Rosehaugh		Evanton	
	1951	1952	1951	1952
No: cones on sample area	110	84	200	40
No: female Megastigmus	927	78	130	313
No: good seeds	3048	2624	2988	599
No: females per cone	8.4	0.9	0.6	7.8
No: females per 100 good seeds	30.4	3.1	4.3	52
Average no: eggs laid per female	1.4	18.3	39.1	1.4
No: Megastigmus larvae	1174	1362	2842	418
No: female Amblymerus	631	212	109	152
No: females per cone	5.7	2.5	0.5	3.8
No: females per 100 host larvae	53.9	15.5	3.8	36.2
Average no: eggs laid per Amblymerus female	0.95	3.1	14.4	1.8

Analysis of Mortality by Bess's Method

Utilising the formuale given in the section dealing with the results at Bedgebury the following tables were constructed.

TABLE 26

Rosehaugh

	1950		1951		1952	
	%	m/s	%	m/s	%	m/s
Parasitism	48.2	0.9	51.1	1.0	48.4	0.9
Mortality due to mice	59.9	1.8	82.1	6.4		
Late larval mortality	6.3	0.2	5.1	0.4		

Evanton

Parasitism	18.9	0.2	39.4	0.6	83.3	5.0
Mortality due to mice	82.8	6.1	88.6	10.4		
Late larval mortality	21.7	1.6	2.7	0.3		

From these mortality/survival ratios the Relative % Equivalents can be calculated

TABLE 27

Rosehaugh

	1950	1951	1952
Approximate density of cones per tree	218	24	18
Relative % Equivalents			
Parasitism	47.7	50.0	47.4
Mice mortality	64.3	86.5	
Late larval mortality	16.7	28.6	

Evanton

Cone density/tree	23	4.5	1.0
Relative % Equivalents			
Parasitism	16.7	37.5	83.3
Mortality by mice	85.9	91.2	
Late larval mortality	61.5	23.1	

A density-dependent control factor whose intensity increases with increase of host density. The figures for 1951 and 1952 in Table 27. taken together with the density of Megastigmus in these years given in Table 25. suggest that Amblymerus is a mortality factor acting in this fashion.

Section (j)

Analysis of field data in the light of Nicholson and Bailey's theories.

The two basic assumptions made by these workers were (1) that parasites search for their hosts at random and (2) that parasites, in their random search for hosts, search an area, termed the area of discovery, the average size of which is constant and/not dependent on the population densities of hosts and parasites.

In his study on Urophora Varley(1947) stated that his data could not be claimed to demonstrate the accuracy of Nicholson and Bailey's assumptions and went on to suggest that it is inconceivable that the area of discovery should remain constant over a wide range of host and parasite densities. As a result of the present study it is possible to present a considerable range of population densities with the appropriate values of the area of discovery calculated.

Although Megastigmus is phytophagous we can consider it as a parasite on Douglas Fir seed and so calculate its area of discovery under different host

densities. Nicholson and Bailey give the area of discovery as $\frac{2.3}{\text{Population density of adult parasites}} \times \log \frac{1}{\text{fraction of hosts unattacked}}$

As the area of foliage which the female Megastigmus must search for cones is difficult to determine with accuracy and bearing in mind that area in a horizontal plane has little meaning when applied to density of cones in a forest all values of density have been expressed per cone. The significance therefore of a "cone" in this sense varies with the size of the cone crop. If 1000 cones grew on 1000 square feet of foliage then 1 cone, in that year, would "occupy" 1 square foot. If the following year the same area supported only 10 cones then 1 cone would "occupy" 100 square feet.

TABLE 28

Area of Discovery of Megastigmus

	Rosehaugh		Evanton		Bedgebury	
	51	52	51	52	51	52
Density females per cone	8.4	0.9	0.6	7.8	3.7	4.9
Fraction of good seed uninfested	.62	.48	.05	.30	.05	.16
Area of discovery per cone	.06	.83	1.2	.16	.19	.37

Area of discovery of Amblymerus

Density ♀♀ per cone	5.7	2.5	0.5	3.8		
Fraction host unattacked	.49	.52	.61	.37		
Area of discovery	.12	.34	.98	.28		

These results show a very definite tendency for the area of discovery to increase with decrease of the density of the parasite relative to the host. It is however interesting to observe that the average area of discovery in both host and parasite, (which are in fact both searching for the same oviposition site) is almost the same.

Average area of discovery of Megastigmus = .47 cones

" " " " " Amblymerus = .43 "

As Varley has pointed out it is possible to use the theory of Nicholson and Bailey to calculate the population density of host and parasite, assuming them to be in the steady state. This condition is said to exist when the host and parasite are in exact equilibrium. The actual densities will naturally oscillate about the steady density as a mean, but the average value of the density over a number of generations should be close to the steady density.

Steady Density of Amblymerus

$$= \frac{2.3}{\text{Area of discovery of Amblymerus (a)}} \times \log. \text{ Natural Rate increase of Megastigmus} \quad (F)$$

TABLE 29

Rate of increase of Megastigmus

	Rosehaugh		Evanton		Pedgebury	
	51	52	51	52	51	52
Larvae/cone	10.7	16.2	14.2	10.4	11.4	11.1
females/ "	8.4	0.9	0.6	7.8	3.7	4.9
Rate of increase	0.6	13.5	12.0	0.9	1.5	1.2

In only two of these cases was the density of female Megastigmus sufficiently low for a true rate of increase to be manifested. In the other figures the increase is masked by the considerable competition for suitable seed. As it is only in good seed years that the crop will be used commercially, or for regeneration, we will take the rate of increase as 13 (Columns 2 and 3 of Table 39). In the steady state 12/13 or 92.3% of the Megastigmus population must be killed-off to balance the 13-fold rate of increase.

The population density of Amblymerus required to parasitize 92.3% of the Megastigmus can be found as follows :-

$$\text{Steady Parasite Density} = \frac{2.3}{a} \times \log.13.$$

$$= \underline{5.8 \text{ per cone}}$$

$$\text{Steady Host Density} = \frac{2.3 \times \log F.}{a(F - 1)}$$

$$= \frac{2.3 \log 13}{.48(13 - 1)}$$

$$= \underline{0.4 \text{ per cone}}$$

The value of the steady density of Megastigmus is below that actually found in the forest but in the above calculations we have assumed that Amblymerus killed 92.3% of its hosts whereas it, in fact, never killed more than 63%.

Other mortality factors affecting the steady state were (a) non-parasitic factors acting only on Megastigmus and (b) non-specific factors acting on both Megastigmus and its parasite.

(a) Specific non-parasitic factors affect the fecundity or mortality at some stage of development. Fecundity may be affected by the weather, during oviposition or, as demonstrated at Bedgebury, upsetting the coincidence between the suitability of the cones for oviposition and the flight period of Megastigmus. A further important factor is the population density of the female Megastigmus as high density reduces fecundity see Table 30.

TABLE 30

	Rosehaugh		Evanton		Bedgebury		
	51	52	51	52	51	52	53
Density of ♀♀ per cone	8.4	0.9	0.6	7.8	3.7	4.9	0.2
Fecundity per female	1.4	18.3	39.1	1.4	11.4	11.1	144.0

These conditions of high density also increase the mortality due to starvation in seeds infected with more than one egg (see Table 17).

(b) The most important non-specific mortality factor acting on both Megastigmus and Amblymerus is that due to damage by rodents. As conifer seed is not the main food of rodents, and so is not sought out by them in preference to other foods, such mortality does not act in a density-dependent fashion on either host or parasite. It is not possible to assign an average value to this factor as it varies with the size of the cone crop and the availability of other food supplies to the mice. Utilising formulae derived by Varley it is, however, possible to determine the effects of different average values of such

mortality upon the balance of host and parasite.

In the steady state 92.3% of the Megastigmus must be killed off but if, following parasitization, the rodents destroy a fixed % of larvae so that a proportion x survives then the parasite will only have to account for $(1 - \frac{1}{13}x)$ instead of 12/13. By following the successive changes in the population densities of host and parasite during one generation Varley deduced the following formulae for the steady densities of host and parasite :-

$$\text{Steady Density of Parasite (p)} = \frac{2.3}{\text{Area of discovery of parasite (a)}} \times \log. \text{Natural Rate of Increase of Host (F)} \times \text{Fraction of hosts escaping attack (x)}$$

$$\text{Steady Density of Host} = \frac{p}{Fx - 1}$$

Substituting values obtained during the present work in these formulae Table.31. was derived. This illustrates the important conclusion that increased severity of rodent attack, in areas where Amblymerus is active, actually serves to increase the density of Megastigmus and decrease that of the parasite.

It is not possible to extend the reasoning of Nicholson and Bailey, as suggested by Varley(1947 and 1953), owing to the fact that observations have covered only three generations of host and parasite.

TABLE 31.

The Theoretical Effects of Different Levels of Mice Predation on balance between Megastigmus and Amblymerus.

% Mortality acting on both host and parasite following parasitization	Steady Density of Megastigmus ♀♀/cone	Steady Density of Amblymerus ♀♀/cone
40%	.63	4.3
70%	.97	2.8
80%	1.30	2.0

(k) Discussion and Conclusions

It should be stressed that bionomic surveys of the type presented in this paper must be interpreted as suggesting indications and trends rather than fixed arithmetical values. Although the sampling technique employed tended to give most accuracy in poor seed-years the uniformity of conditions within the cones, in any single year, gave the computed averages considerable accuracy. The largest source of error involved arose in assessing the mortality due to mice. It was not possible to sample large areas of litter owing to the time required to analyse the duff. However the fact that the % mortality calculated in the three areas were of the same order suggests that it is of the correct order of magnitude.

The study has demonstrated the value of seed-infesting insects for bionomic investigations as the total population is calculable within narrow limits and the various mortality factors can be assessed at all stages of insect development.

The forester is naturally concerned with the amount of good, fertile, seed which he may expect in any given year. The relevant information illustrating the factors influencing the proportion of seed which he is liable to lose as a result of Megastigmus attack will now be considered.

The females are on the wing for about three weeks and will, under conditions of low density relative to the cones, lay about 150 eggs in good fertile seeds. The number of females which oviposit in the Spring

is determined by (1) the number of larvae completing prolonged diapause from the penultimate crop (2) the size of the cone crop of the previous year (3) the % of larvae remaining in prolonged diapause and (4) the % infestation of the seed in that previous crop. Diapause studies suggest that there is a constant proportion, about 10%, in which the tendency to long diapause is genetically fixed. In addition emergence of a further fraction of the population is governed by the spring weather conditions, especially temperature. There seems to be a larger % remaining in diapause in North Scotland than in England - 40% as against 20%. This fairly general pattern may on occasion be upset e.g. Evanton in 1950 when 83% of the larvae remained in diapause. It is suggested that the conditions prevailing at the time of oviposition may influence the diapause factor in the larvae through a stimulus affecting the female. This could be due to a very low Megastigmus/host density for it has already been shown that a high density tends to alter the sex-ratio.

A good seed-year following a series of poor years should tend to reduce the % of infection if the % undergoing prolonged diapause remains constant. Such a premise should occur when the good seed-years are widely separated for, normally, the Megastigmus population will tend to fall with successive poor crops.

However, the high level of infection expected from a high density of females/cone may be reduced in an

early or a late spring by the lack of synchronisation between the suitability of the cones and the adult flight period. The cones are only susceptible to attack by Megastigmus for 2-3 weeks and their phenology is less affected by temperature deviations from the mean than is that of the insect. No difference in seed infection could be traced to variations in the height of the cones above the ground - any reduction in the number of eggs/seed probably being due to a higher cone density per unit area at the tops of the trees where the bulk of the cones occur.

It has been demonstrated that the larvae, which consume the host seed within 7 weeks, are very resistant to heat and cold so that climatic mortality is most unlikely. Egg mortality during the survey was also insignificant. The most important mortality factors dependent on density were (a) Mortality due to more than one egg being laid in a single seed as only one larva can complete development on the available nutriment and (b) mortality due to the shrinkage of unfertilised seed. In poor cone years there was a decrease in the disease mortality resulting from a wider dispersal of the larvae. It is evident however that the nature of the secluded microhabitats within the seeds is such as to reduce the possibility of major outbreaks of didease organisms even under conditions of high larval density. As Varley(1947) has pointed out density-dependent larval mortality acting alone would not prevent 100% of the host units becoming infected.

Mortality of the larvae due to predation by mice accounts for a considerable % of the Megastigmus population but this factor is not dependent on density and so is not functional in keeping the insect population in balance. Furthermore it has been demonstrated earlier that, where the parasite Amblymerus is present, the effect of indiscriminate mice predation is to increase the density of the pest and decrease that of the parasite.

Although there is some evidence that mice tend to take preferentially those seeds which contain Megastigmus larvae the net effect of their activities is only to reduce the numbers of larvae surviving irrespective of their density on the ground.

It is instructive to combine data from all the surveys showing the Relative Percentage Equivalents for the various mortality factors together with host density as in Table 32.

TABLE 32.

No; cones per tree	232	104	52	218	24	18	23	4.5
Relative % Equiv: Mice Damage	76.7	71.5	56	86.5	-	-	91	-
Late larval mortality	85.0	74.2	58	61.5	23	-	16	29
Density parasites per 100 larvae	53.9	11.7	3.8	18.8				
Rel: % Equiv: Parasitism	50.0	47.4	38	83.3				

These results illustrate the relative constancy of the mice control factor over a 10-fold change in cone density. They also show that late larval

mortality is much less effective at low host densities.

Where Amblymerus occurs the overall infection of potentially sound seed by Megastigmus was only of the order of 50% although the population density of the pest was at times higher than at Bedgebury where, in the absence of the parasite, infection reached 98%. The average fecundity of Amblymerus on the areas studied was 40 eggs/female which was considerably below that of Megastigmus but in no case was the female density low enough to allow uninhibited oviposition. The long life and delayed ripening of the ovarioles of the parasite resulted in their being less subject to weather conditions at oviposition than Megastigmus. Emerging in mid-September they await the opening of the cone scales to allow access to the infested seed. Like Megastigmus they are profoundly influenced as regards oviposition by the density of females per host. Also, like its host, Amblymerus is adapted to the irregular fluctuations in the density of the oviposition habitat by the extended diapause of part of the population. During the survey the extent of this diapause varied in approximately the same manner as in Megastigmus in the same area.

It is demonstrated that, as well as having similar fecundities, host and parasite have the same area of discoveries over a wide range of densities. These facts indicate that the host would have little opportunity of increasing more rapidly than the parasite. Reference to Table 32. shows

that the Relative % Equivalents for parasitism remain almost the same at Rosehaugh despite a 5-fold fall in parasite/host density but that at Evanton a 5-fold increase in this density enabled parasitism to reach 63%. It is postulated that the low level of parasitism at Rosehaugh in 1951 was caused by two factors. (1) The exceptionally high parasite population of 54 females/100 host larvae which drastically curtailed the oviposition rate and (2) an early and rapid seed/fall which further hindered egg deposition. It should be observed that, where parasites were present, seed infection was less, so that the parasite deserves introduction into fresh areas. Hanson (1951) has suggested that a suitable parasite might be used for economic control in this manner. Introduction could be achieved by collecting cones within the present range of the parasite and placing them, protected from mice, below infested stands. During mid-May to mid-June such cones should be covered to cause starvation, without oviposition, of the emergent unparasitized Megastigmus. Such cones left in situ will release the parasites in the fall.

In the field of pure science the paper presents evidence (in Tables 28 and 29) that the value of the area of discovery of a parasite is not constant over a wide range of host and parasite densities as Varley(1947) postulated on theoretical grounds.

We are fortunate that our most serious seed pests M.spermotrophus and M.pinus affect only Abies spp. and Douglas Fir which have not been widely used in our

afforestation programme. There is no reason to suppose however, that M.seitneri on Larch and M.strobilobius on Spruce will not become as widespread and injurious. In such an event the discovery of suitable parasites will be essential to prevent disruption of management plans.

Chapter IX

Distribution of Megastigmus species

Distribution was investigated by examining all the samples of tree seed held by the seed testing stations at East Craigs, Edinburgh and the Institute of Agricultural Botany at Cambridge. In addition seed-lots handled by the extraction plants of the Forestry Commission at Tulliallan, Fife; Newton, Elgin; Santon Downham, Norfolk; Grizedale, Westmoreland; Parkend, Gloucestershire; and Kirkton, Aberdeenshire were examined.

Numerous samples were brought to my notice privately by officers of the Commission and following the registration of the Research Station at Alice Holt as a seed testing unit in 1951 further records became available. The results of a survey of Douglas Fir seed by the Entomological Branch in 1950 were also placed at the writer's disposal.

On the collation of this material the appended distribution maps were built up. Apart from the information obtained on indigenous species some data were prepared on the importation of infected seed from abroad. A sample was said to be infected if any of the seeds had exit-holes in the testa. In many instances dead adults were found. Table 33 has been built up from this information.

As can be seen from the maps M.spermotrophus is widespread in Douglas Fir but it should be remembered that as many of the samples were small a "no infection"

record does not necessarily indicate beyond doubt that the species is absent,. M.pinus is present in most Scottish stands but only a few English samples were received. M.seitneri was found at Dunkeld and Bedgebury. M.rafni was reared from Silver Fir seed from Kincardineshire whilst M.milleri was obtained from A.grandis at Evanton. The information on M.strobilobius is indefinite as adults were not reared in the survey. Gillanders(1912) records a Mr. Forbes as obtaining it from Longleat Park, Wilts and Ritchie (1920) records it from A.grandis at Dumfries. This latter record is suspect and I imagine that M.pinus or M.suspectus was the species involved. Laidlaw(1931) mentions that Dr.Scott recorded M.strobilobius from Co.Wicklow,Ireland. There is a record in this Department of larvae in Norway Spruce seed from Philiphaugh,Selkirk; and a larva was found in a tube labelled Grizedale Forest. All these areas were sampled without success. A Commission sample from Dalswinton Estate,Dumfries was found to contain larvae but further sampling by Hanson and myself failed to confirm the record.

M.suspectus is often reared in imported seed from the Continent but the only definite record of its breeding here is that of McNeill(1946) who obtained it from A.grandis at Orton,Morayshire.

TABLE 33

Tree Species	Megastigmus spp.	Origin
Douglas Fir	M.spermotrophus	U.S.A.(12) Denmark(1) British Columbia(1)
Abies grandis	M.milleri	U.S.A.(1)
A.nordmanniana	M.suspectus	Austria(1)
A.veitchii	?	Japan(1)
European Larch	M.seitneri	Switzerland(1)
Japanese ,,	M.inamurae	Japan (42)
Norway Spruce	M.strobilobius	France(5) Austria(20)
Sitka Spruce	M.piceae	U.S.A.(2) British Columbia(8)
P.engelmanni	,,	U.S.A.(1)

Acknowledgements

My thanks are due to Mr.H.S.Hanson and Mr.M.V. Laurie,who suggested the project and arranged a grant from the Forestry Commission to cover travelling expenses, and to Mr.J.W.McHardy under whose general direction the study was conducted.

A special word of thanks is due to the many officers and foresters of the Commission who did so much to provide the many samples required. Mr.A. Westall and Mr.F.Barrow of Bedgebury,Mr.Patience of Avoch and Mr.Ross of Evanton deserve special mention along with Novar and Atholl estates.

Appendix 1

Census at Pedgebury, Kent

(i) Spring 1950

Total number of young cones available for oviposition = 9396

No: seeds/cone	62	48	60	42	34	62	60	64	50	56	44	66	78	66	52
No: good seeds	2	6	5	4	4	9	8	10	1	9	5	8	1	12	13
No: shrunken	60	42	55	38	30	53	52	54	49	47	39	58	65	54	39

Therefore Average No:Seeds/cone = 56.3±2.9 ✓

% Seeds Naturally shrunk = 87.0±1.5 ✓

% Seeds suitable for oviposition = 13.0±0.9 ✓

Number of embryos from good seed examined 96
" " " infested with Megastigmus 94

% Good Seed Infested = 98.0% ✓

% seed infested with 1 egg/seed = 97.8% (See Table 16)

" " " " 2 " " = 2.2%

Number of embryos from shrunken seed examined 58
" " " infested 0

% Shrunken Seed Infested 0% ✓

(ii) Spring 1952

Total Cones 4143

No: seeds/cone	70	79	81	89	84	74	84	71	79	79
No: good seeds	5	14	6	16	15	8	17	15	13	11
No: shrunken	65	65	75	73	69	66	67	56	66	68

Therefore Average Number Seeds/cone = 79.0±2.4 ✓

% seeds naturally shrunk = 84.8±1.6 ✓

% seeds suitable for oviposition = 15.2 ✓

Number of embryos from good seed examined 637
" " " infested 605

% Good Seed Infested = 95.0±2.8

% Seed infested with 1 egg/seed = 86.8±4.9 (See Table 16) ✓

% Seed infested with 2 eggs/seed = 9.1±3.0
" " " " 3 " " = 2.5±1.0
" " " " 4 " " = 1.7±1.6

Number of embryos from Shrunken seed examined 527
" " " " " " infested 198

% Shrunken Seed Infested = 37.6±4.8 ✓

% Shrunken seed with 1 egg/seed = 94.8 (Table 16)
" " " " 2 " " = 5.2
" " " " 3 " " = 5.2

Number of 1950 cones remaining on trees = 8406

23 of these cones contained 145 seeds = 6.3±1.6/cone ✓

No: of infested seeds = 77

No: larvae dead = 4 = 5.2±3.6% ✓

No: larvae in extended diapause = 21 = 27.3±3.4% ✓

No: pupae dead = 0 = 0%

Number of 1950 cones fallen to ground overwinter = 990

134 cones contained 2560 seeds = 19.1±3.6/cone ✓

No: of infested seeds = 546 =

No; larvae dead = 53 = 9.7±2.9% ✓
No: larvae in extended diapause = 112 = 22.7±6.0% ✓

No: pupae dead = 22 = 6.5±3.1% ✓

Mean larval mortality based on above figures = 7.4%

Mean Pupal mortality " " " " = 3.2%

Mean % larvae in extended diapause = 25.0%

Total Number of adults reared from 1950 seeds was

207 males and 315 females therefore sex ratio = .60 ✓

Litter Sampling 1951

Undamaged Seed																				
Shrunken	10	9	7	7	8	77	7	8	6	7	9	5	8	5	4	8	6	3	8	11
Seed + exit holes	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0
Seed * larvae	1	2	0	0	0	1	1	0	1	1	2	0	0	1	0	0	0	1	0	0

Damaged Seed

Shrunken	3	2	1	2	1	1	2	2	1	1	1	3	1	3	5	2	1	1	2	1	
Seed + larvae	0	4	2	2	1	3	2	1	2	2	0	4	1	1	2	2	2	1	1	0	

Undamaged Seeds

Total Shrunken	143
,, Seed + Exit Holes	4
,, Seed + Larvae	11

Damaged Seed

Total Shrunken	36
,, Seed + Larvae	33

% Seed Damaged 30.4±1.3 ✓

% Seed, infested by Megastigmus, damaged 68.8±6.2 ✓

(iii) Spring 1952

Total cones available for oviposition 2094

No: seeds/cone	74	80	71	93	65	58	69	60	70	62	88	77 =867
No: good seeds	—	—	15	24	10	15	13	12	14	10	22	31 =166
No: shrunken	—	—	56	69	55	43	56	48	56	52	66	46 = [illegible] 547

No: seeds/cone	74	74	80	88	84	80	78	78	80	110	= 826
No: good seeds	14	16	11	5	9	8	6	5	6	17	= 97
No: shrunken	60	58	69	83	75	72	72	73	74	93	= 729

Therefore Average Number Seeds/cone =77.0±2.3

% Seeds naturally shrunk =82.9±2.2

% Seeds [illegible]table for oviposition =17.1

Number of embryos of good seed examined = ~~382~~ 352

,, ,, ,, ,, ,, ,, infested = 301

% Good Seed Infested 83.8 4.5 ✓

% seed infested with 1 egg/seed 55.4±8.6 (See Table 16)

,, ,, ,, ,, 2 ,, ,, 30.4±5.7

,, ,, ,, ,, 3 ,, ,, 8.4±2.2

,, ,, ,, ,, 4 ,, ,, 4.0±1.5

,, ,, ,, ,, 5 ,, ,, 1.0±0.6

,, ,, ,, ,, 6 ,, ,, 0.7±0.3

Number of embryos of shrunken seed examined 74

,, ,, ,, ,, ,, ,, ,, 36

% shrunken seed infested 48.6±7.0 ✓

% Shrunken Seed with 1 egg/seed = 72.2 ✓
" " " " 2 " " = 25.0 ✓
" " " " 3 " " = 2.8 ✓

Number of 1951 cones remaining on trees = 3571

29 of these cones contained 394 seeds = 10.1/cone ✓

No: infested seeds = 268

No; larvae dead = 8 = 3.0% ✓

No: larvae in extended diapause = 132 = 49.3% ✓

No: pupae dead = 2 = 0.7% ✓

Number of 1951 cones fallen to ground overwinter = 572

80 of these cones contained 974 seeds = 12.2/cone ✓

No: infested seeds = 98

No: larvae dead = 1 = 1.0% ✓

No: larvae in extended diapause = 9 = 9.2% ✓

No: pupae dead = 1 = 1.0% ✓

Mean larval mortality based on above figures = 2.0% ✓

Mean Pupal mortality " " " " = 0.7% ✓

Mean % larvae in extended diapause = 29.2% ✓

Total number adults reared from 1951 seed was

46 males and 112 females therefore sex-ratio = .71 ✓

Litter Sampling 1952

Undamaged Seed																				
Shrunken	2	1	0	0	0	0	3	3	5	6	4	2	1	5	3	8	7	5	0	0
Seed + exit holes	0	0	0	0	0	0	3	3	1	0	1	1	0	2	1	0	0	0	0	0
Seed + larvae	0	0	0	0	0	0	1	0	1	1	1	1	0	0	2	2	3	1	0	1
Damaged Seed																				
Shrunken	0	0	0	0	0	0	3	3	0	2	0	1	1	1	2	1	0	0	1	1
Seed + larvae	0	0	0	0	0	0	1	3	2	2	2	4	2	1	0	3	0	0	0	0

Undamaged seeds

Total shrunken	55
" Seed + Exit Holes	12
" Seed + larvae	14

Damaged Seed

Total shrunken	16
" seed + larvae	21

% Seed Damaged 31.4±14.5

% Seed, infested by Megastigmus damaged 60.0±10.6

(iv) Spring 1953

Total number of young cones available for oviposition 9348

As this was an "early" year the cones of P.glauca were attacked first so that, for accuracy, the two forms are dealt with separately.

Cones of P.glauca = 2870

Cones of P.douglasii = 6478

P.douglasii

No: seeds/cone	72	71	69	70	70	72	68	64	76	70	70	74
	72	77	72	67	77	75	60	62	62	72	74	68
	64	77	75	70	78	77						
No: good seeds	27	20	15	16	18	21	15	16	22	23	20	19
	18	23	20	21	10	26	20	17	20	18	15	16
	22	21	19	18	21	22						
No: shrunken	45	51	54	54	52	51	53	48	54	47	50	55
	54	54	52	46	67	49	40	45	42	54	59	52
	42	56	56	57	55	55						

1549
2125

Therefore Average Number seeds/cone 70.8±0.9

% seeds naturally shrunk 72.8±1.0

% seeds suitable for oviposition 27.2±1.0

P.glauca

No: seeds/cone	72	74	75	74	80	77	75	77	76	86	77	84
	64	75	72	74	70	80	77	85	78	77	85	83
	74	76	84	70	74	74						
No: good seeds	25	21	23	21	21	30	28	29	25	30	25	22
	15	14	27	26	25	24	33	28	21	26	22	30
	29	26	24	31	25	27	30					
No: shrunken	47	53	52	53	59	47	49	46	51	56	52	54
	69	50	48	46	49	46	47	49	64	52	55	55
	54	58	52	53	45	47	30					

2225/29.

1558.

Therefore Average No: seeds/cone 76.7±0.8

% seeds naturally shrunk 67.2±1.0

% seeds suitable for oviposition 32.8±1.0

Therefore number good seeds available for oviposition

P.douglasii 6478 x 70.8 x .272 = 124751

P.glauca 2870 x 76.7 x .328 = 72202

number shrunken seeds

P.douglasii = 333891

P.glauca = 147927

Number of eggs found in dissected seeds :-

P.~~douglasii~~ glauca

	Good seeds with				
0	1	2	3	4	eggs/seed
14	229	259	82	48	

	Shrunken seed		
392	168	28	0	0

P.douglasii

	Good seeds with			
0	1	2	3	4
610	101	0	0	0

	Shrunken Seed			
526	0	0	0	0

Therefore % seeds attacked by Megastigmus

P.glauca

% good seed attacked = 97.8±0.6 ✓

% shrunken seed attacked = 33.3±1.9 ✓

P.douglasii

% good seed attacked = 14.2±1.3 ✓

% shrunken seed attacked = Nil

% Seeds with various numbers of eggs

P.glauca

Good Seed

229 seeds with 1 egg = 37.1%
259 ,, ,, 2 ,, = 41.9%
82 ,, ,, 3 ,, = 13.3%
48 ,, ,, 4 ,, = 7.7%

Shrunken Seeds

168 seeds with 1 egg = 85.7%
28 ,, ,, 2 ,, = 14.3%

P.douglasii

Good Seed

101 seeds with 1 egg = 100%

Shrunken Seed

Nil

Eggs laid per 100 seeds

P.glauca

Good Seed 32.8			Shrunken seed 67.2		
97.8% attacked by Megastigmus			33.3% attacked		
Therefore 32.1 seeds with eggs			Therefore 22.4 with eggs		
37.1% with 1 egg	= 11.9 eggs		85.7% with 1 egg	= 19.2 eggs	
41.9% ,, 2 ,,	= 26.9 ,,		14.3% ,, 2 ,,	= 6.4 ,,	
13.3% ,, 3 ,,	= 12.8 ,,				
7.7% ,, 4 ,,	= 9.9 ,,				
Total	61.5			25.6	

P.douglasii

Good Seed 27.2		Shrunken Seed 72.8
14.2% attacked by Megastigmus		
Therefore 3.9 seeds with eggs		Nil
100% with 1 egg	= 3.9 eggs	

Examination of Trapped Seed

No: infested seeds = 558

No; larvae dead = 9 = 1.6±0.5 % ✓

No: larvae in extended diapause = 150 =27.3±0.6% ✓

No: pupae dead = 0 = 0%

Mean Larval Mortality 1.6%

Mean Pupal Mortality 0%

Mean % larvae in extended diapause 27.3%

Total number of adults reared from 1952 seed was

209 males and 190 females therefore sex-ratio = .48

Litter Sampling 1953

Undamaged Seed																			
Shrunken	5	2	4	0	1	3	0	3	5	7	3	1	2	0	4	3	3	3	4	1
Seed + Exit Holes	0	1	1	3	0	0	0	1	0	0	0	0	0	0	0	1	1	0	0	1
Seed + larvae	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0	0
Good Seed	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0	1	0
Damaged Seed																				
Shrunken	0	0	0	1	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0
Seed + larvae	0	2	0	1	1	1	1	2	0	0	0	0	1	0	0	1	1	2	0	0

Undamaged Seed	
Total Shrunken	54
,, Seed + Exit Holes	9
,, Seed + larvae	4
,, Good Seed	4
Damaged Seed	
Total Shrunken	5
,, Seed + Larvae	13

% Seed Damaged 20.2±4.4 ✓

% Seed, infested by Megastigmus, damaged 50.0±9.8 ✓

Appendix 11

Census at Rosehaugh, Black Isle, Ross.

1950

Cone Counts on sample area = 653

No: seeds/cone 68 72 68 96 86 72 68 94 86 96 72 88
66 84 114 74 94 64 80 74

Average number seeds/cone 80.8±3.0

Dissections

Shrunk	Good	Good seed + larvae
617	59	232

% good seed in total = 32.0±1.6

% good seed infested by Megastigmus 79.7±2.4

Late larval mortality

Megastigmus		Amblymerus	
Alive	Dead	Alive	Dead
152	27	123	21
% Mortality		Mortality	
15.1±8.4		14.6±2.9	

Emergences

	Megastigmus	Amblymerus
1951	482 males 234 females	302 males 195 females
1952	393 ,, 309 ,,	527 ,, 309 ,,

Therefore % Extended Diapause

51.3±1.3	62.7±4.2

Sex - Ratio

0.4	0.38

Parasitism

Megastigmus unattacked	1547
Amblymerus	1477
Anogmus	42

Therefore % Parasitism by Amblymerus = 48.2±0.9

% ,, ,, Anogmus = 1.4

1951

Cone counts on sample area = 71

No: seeds/cone 96 104 98 100 84 86 80 80 72 64 70 84 82
90 96 108 96 112 104 66 80 104 76 50 72
76 76 106 84 94 100 70 88 80 74

85.8

Average Number of Seeds/cone 82.9±1.2

Dissections

Shrunk	Good	Good seed + larvae
1367	401	250

% Good Seed in Total 32.3±1.0

% Good seed infested by Megastigmus 38.4±1.9

Late Larval Mortality

Megastigmus		Amblymerus	
Alive	Dead	Alive	Dead
60	4	60	1
% Mortality		% Mortality	
6.3±3.0		1.6±1.2	

Emergences

Megastigmus	Amblymerus
1952 53 males 13 females	40 males 40 females
96 larvae	95 larvae

Therefore % Extended Diapause

59.3±3.9	54.3±3.8

Sex - Ratio

0.2	0.5

Parasitism

Megastigmus unattacked	226
Amblymerus	236

Therefore % Parasitism by Amblymerus 51.1±2.3

1952

Cone counts on sample area = 54

No: seeds/cone 76 80 76 78 84 90 60 78 80 64 88 76
96 114 80 94 110 70 76 74 84 78 102
82 74 80

Average number seeds/cone 82.5±2.4

Dissections

Shrunk	Good	Good seed + larvae
1297	380	410

% Good seed in total = 37.9±1.1

% Good seed infested with Megastigmus 51.9±1.8

Late Larval Mortality

Megastigmus		Amblymerus	
Alive	Dead	Alive	Dead
332	18	58	1
% Mortality		% Mortality	
5.1±1.2		1.7±0.5	

Parasitism

Megastigmus unattacked	192
Amblymerus	180

% Parasitism = 48.4±2.1

Litter Samples

1951

Undamaged												
Shrunk	6	5	5	11	49	20	1	12	24	17	=	150
Good	0	0	0	1	1	0	0	0	1	0	=	3
Seed + Megastigmus	0	1	1	1	11	5	3	1	5	4	=	32
,, + Amblymerus	0	0	1	2	1	0	0	0	2	0	=	6
Damaged by mice												
Shrunk	3	1	0	1	21	5	0	2	3	4	=	40
Good	0	0	0	0	0	0	0	0	0	0	=	0
Seed + Megastigmus	1	1	1	3	2	3	2	1	2	1	=	17

Total Undamaged = 191
,, Damaged = 57
Therefore ,, carried off = 228

Loss due to mice = 59.9±2.2

1952

Undamaged												
Shrunk	18	8	14	23	7	11	5	4	8	8	=	106
Good seed	1	0	0	0	0	0	0	0	1	0	=	2
Seed + Megastigmus	1	0	4	7	2	2	0	6	2	4	=	28
Damaged												
Shrunk	2	12	1	38	6	10	2	12	7	5	=	95
Good seed	0	0	0	0	0	0	0	0	0	0	=	0
Seed + Megastigmus	3	4	1	7	3	2	1	1	5	3	=	30

Total Undamaged = 136
" Damaged = 125
Therefore " carried off = 500

Loss due to mice = 82.1±1.4

Appendix 111

Census at Novar Estate, Evanton, Ross.

1950

Cone counts on sample area = 465

No: seeds/cone 64 84 88 80 110 76 108 96 92 88 76
92 80 68 72 106 68 92 82

Average number seeds/cone 85.4±3.0

Dissections

Shrunk	Good	Good seed + larvae
573	369	68

% Good seed in total = 43.3±1.6 ✓

% Good seed infested by Megastigmus 15.6±1.7 ✓

Emergences

	Megastigmus		Amblymerus	
1951	32 males	18 females	26 males	25 females
1952	79 ,,	165 ,,	17 ,,	16 ,,

Therefore % extended diapause

Megastigmus	Amblymerus
83.0±2.2	39.3±0.2

Sex - Ratio

Megastigmus	Amblymerus
0.62 ✓	0.49 ✓

Late Larval Mortality

Megastigmus		Amblymerus	
Alive	Dead	Alive	Dead
72	20	56	0
% Mortality		% Mortality	
21.7±5.2 ✓		0% ✓	

Parasitism

Megastigmus unattacked	404
Amblymerus	94

% Parasitism by Amblymerus 18.9±1.7 ✓

1951

Cone count on sample area = 91

No: seeds/cone 72 58 72 68 72 56 52 74 82 66 62 84 68
82 78 56 60 64 58 72 60 56 92 92 66 70
72 88 84 64

Average number seeds/cone 69.8±3.0

Dissections

Shrunk	Good	Good seed + larvae
1115	15	289

% Good seed in total = 21.4±1.1

% Good Seed infested by Megastigmus 95.1±1.2

Late Larval Mortality

Megastigmus		Amblymerus	
Alive	Dead	Alive	Dead
33	1	78	1

% Mortality	% Mortality
2.9±2.8	1.3±1.2

Emergences

	Megastigmus	Amblymerus
1952	17 males 31 females 38 larvae	13 males 15 females 27 larvae

Therefore % Extended diapause

44.2±9.5	49.1±6.7

Sex - Ratio

0.65	0.54

Parasitism

Megastigmus unattacked	120
Amblymerus	78

Therefore % Parasitism by Amblymerus 39.4±3.5

1952

Cone counts on sample area = 17

No: seeds/cone 80 56 70 80 62 60 60 66 64 56 68 82 72
66 86 104 86 74 78 84 82 62 82 96 82 70
78 76 84 70 92 84 68 78 98 90 96

Average number of seeds/cone 76.8±3.8

Dissections

Shrunk	Good	Good seed + larvae
1898	141	324

% Good seed in Total = 19.7±0.8

% Good Seed infested by Megstigmus 69.7±2.1

Parasitism

Megastigmus unattacked = 93
Amblymerus = 159

% Parasitism by Amblymerus 63.1%

Litter Samples

1951

Undamaged													
Shrunken	1	0	0	1	3	13	5	1	2	16	=	42	
Good seed	0	0	0	0	0	0	0	0	0	0	=	0	
Seed + Megastigmus	0	0	0	0	1	3	0	0	1	4	=	9	
Damaged													
Shrunken	0	2	0	1	0	14	1	3	2	12	=	35	
Good seed	0	0	0	0	0	0	0	0	0	0	=	0	
Seed + Megastigmus	0	0	2	1	0	5	1	2	1	2	=	14	

Total undamaged = 51
,, damaged = 49
Therefore,, carried off = 196

Loss due to mice 82.8±3.5

1952

Undamaged												
Shrunken	14	10	12	4	10	9	6	7	1	2	=	75
Good	0	0	0	1	0	0	1	0	0	0	=	2
Seed + Megastigmus larva	1	0	1	0	1	1	1	1	0	1	=	7
Damaged												
Shrunken	25	15	20	15	5	6	14	8	1	4	=	113
Good	0	0	0	0	0	0	0	0	0	0	=	0
Seed + Megastigmus larva	1	2	2	2	3	2	2	1	2	1	=	18

Total undamaged = 84
,, damaged = 131
Therefore,, carried off = 524

Loss due to mice 88.6±1.2

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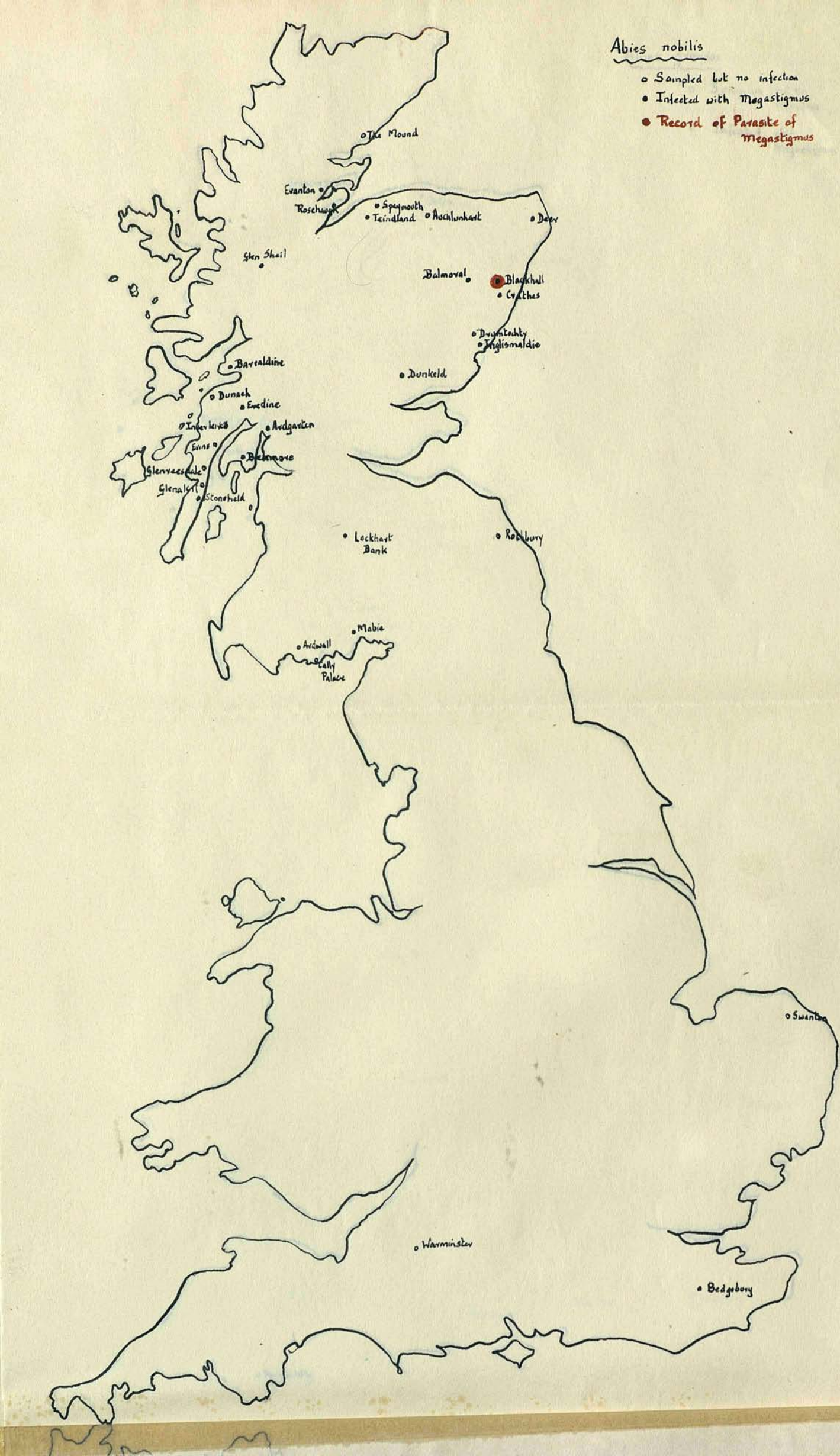
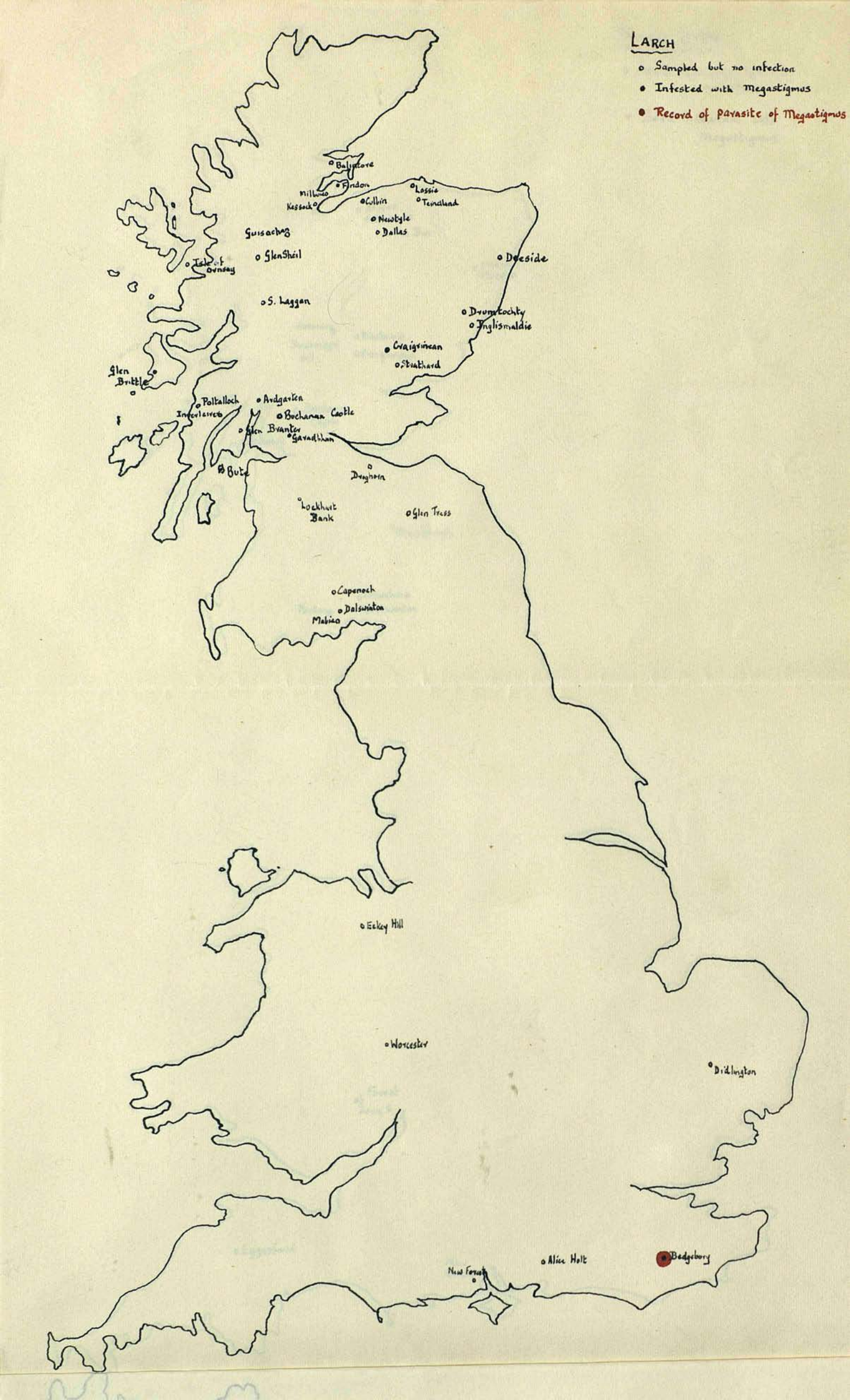
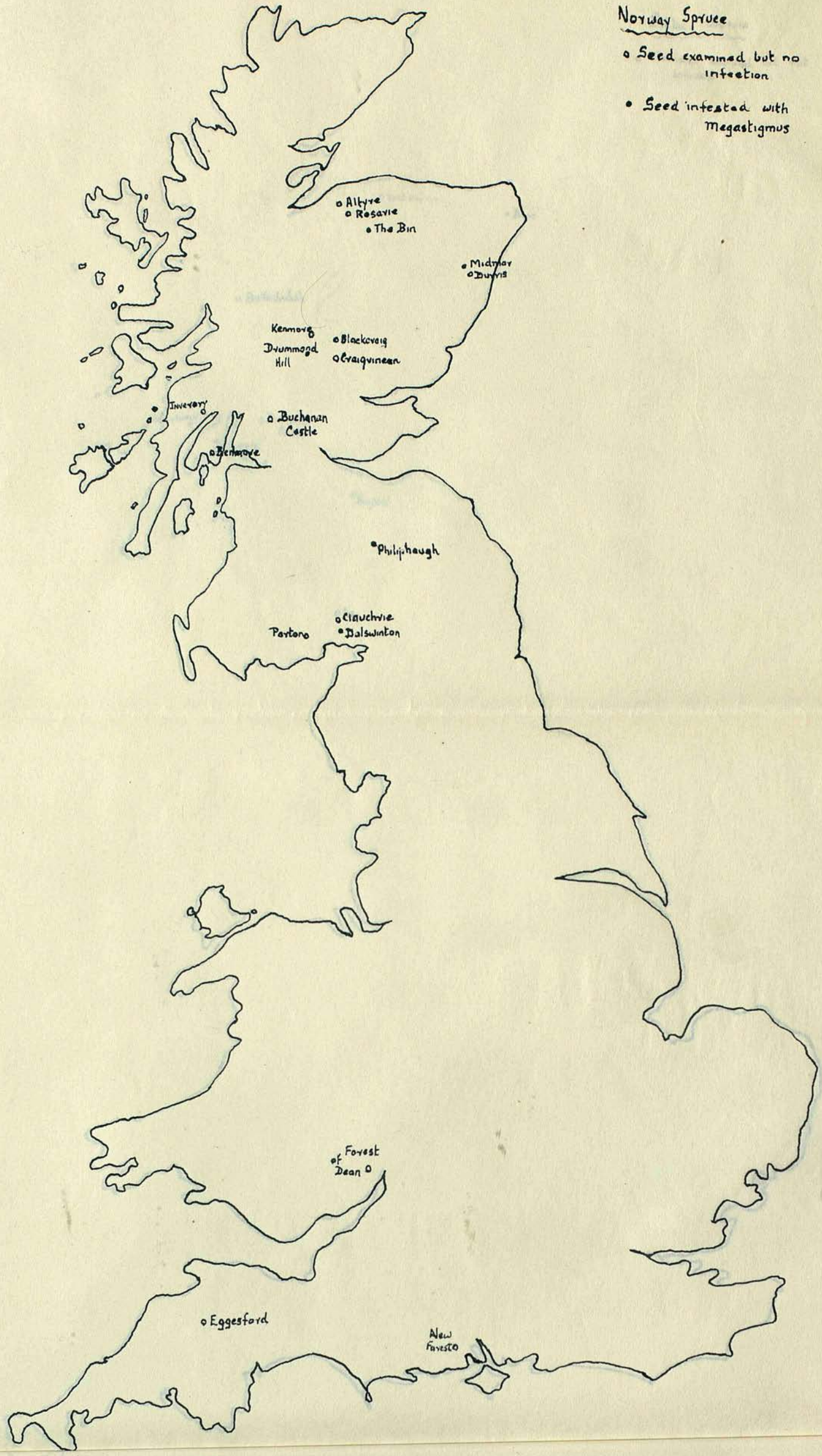
Douglas Fir
Sampled but no infection
Infested with Megastigmus
Record of Parasite of Megastigmus
Amblymerus ? apicalis
Everton
Evaigphadrig
Inverewe
Balmoral
Ballogie
Durris
Blackhall
Evathes
Inglismaldie
Garscadine
Loch Awe
Blackwood
Lockhart Bank
Glen Trees
Elibank
Gresline
Thornthwaite
Thirlmere
Grizedale
Delamere
Walcot
Mortimer
Kevry
Radnor
Dalby
Sandringham
Shouldham
Santon Downham
Thetford
Dedlington
Bedford
Parkhill
High Meadow
Blagdon
Mendip
Brendon
Bruton
Longleat Pk.
Alice Holt
Chiddingfold
Hemsted
Bedgebury
New Forest
Halwill
Templewood
Haldon


Abies nobilis
Sampled but no infection
Infected with Megastigmus
Record of Parasite of Megastigmus
The Mound
Evanton
Rosehaugh
Speymouth
Teindland
Auchlunkart
Deer
Glen Shiel
Balmoral
Blackhall
Crathes
Drumtochty
Inglismaldie
Barraldine
Dunkeld
Dunach
Ewedine
Invergarry
Ardgarten
Erins
Glenreasdale
Glenalvil
Stonefield
Lockhart Bank
Roxburgh
Mabie
Ardwall
Lilly Palace
Swanton
Warminster
Bedgebury


Abies grandis
o Sampled but no infection
• Infested with Megastigmus
Evanton
Orton
Inveraray
Ardhallow
Fernworthy


LARCH
Sampled but no infection
Infested with Megastigmus
Record of parasite of Megastigmus
Ballintore
Findon
Millbuie
Kessock
Culbin
Lossie
Tomaland
Newtyle
Dallas
Guisachan
Glenshiel
Isle of Ornsay
Deeside
S. Laggan
Drumtochty
Inglismaldie
Craigvinean
Strathard
Glen Brittle
Poltalloch
Ardgarten
Inverlaired
Buchanan Castle
Glen Branter
Garadhban
Bute
Drayhorn
Lockhart Bank
Glen Tress
Capenoch
Dalswinton
Mabie
Eskey Hill
Worcester
Didlington
Alice Holt
Bedgebury
New Forest


Norway Spruce
○ Seed examined but no infection
• Seed infested with Megastigmus
○ Alltyre
○ Rosavie
• The Bin
• Midmar
○ Durris
Kenmore
Drummond Hill
○ Blackcraig
○ Craigvinean
Inveraray
○ Buchanan Castle
○ Benmore
• Philiphaugh
○ Clauchrie
Portoro
• Dalswinton
○ Forest of Dean
○ Eggesford
New Forest


Sitka Spruce
o Samples examined but not infected
Orton
Deer
Ballachulish
Inverlochy
Buchanan Castle
Benmore
Boyhall
Ae


Scots Pine
o Sampled but not infected
Rhidorroch
Kessack
Culbin
Cawdor
Newbyle
Assich
Dallas
Lossie
Teindland
Scatfield
Raasay
Guisachan
Queens
Deeside
South Laggan
Poltalloch
Glen Brantey
Buchanan Ces.
Garvaldhan
Glen Tress
Fleet